A TEXT BOOK OF

PLANT ANATOMY

[For B.Sc. (Pass & Agri.)]

BY

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CHANDIGARH

SEVENTH REVISED EDITION

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PREFACE TO THE SEVENTH EDITION

In preparing the present edition, the book has been thoroughly revised and some new matter has been added. The role of anatomy in phylogeny has been discussed in chapter 4. Physiological, environmental and genetical control of differentiation have been discussed in chapter one. This topic is an important addition and throws light on various aspects of plant development and differentiation of tissues.

A number of new illustrations have been added so as to make the description more explicit and understandable. Many figures have been redrawn under the camera lucida so as to bring forth the actual details of the cells and tissues. Much care has been taken to draw the actual shape of the cells. Most of the foreign examples have been replaced by Indian examples so as to make the book suitable for Indian students.

The author has received many useful suggestions from the colleagues all over India. His indebtedness is expressed separately under the acknowledgement.

July, 1977 P.C. Vasishta

PREFACE TO THE FIRST EDITION

The study of plant anatomy is essential for all the students of botany as it acquaints us with the internal set-up of the plant body and forms a basis for the study of other disciplines of botany. With the invention of modern and sophisticated instruments and new techniques, it has now become possible to reveal and expose the intricacies of the internal organisation of the plant It is a pleasure to observe a thin and a well-stained preparation of a part of a plant organ under the microscope. It reveals a striking pattern of arrangement and a complex and orderly internal organisation of the tissue and tissue systems.

The purpose of this book is to introduce this subject to the beginners. The subject-matter has been carefully designed so as to make it understandable to the students. The first chapter gives a brief description of the plant body. The student is introduced to the terms primary and secondary body, and an outline sketch of the development of plant body is given. The chapters two, three and four are devoted to cell structure and division. These chapters reveal, in nutshell, the strikingly complex and intricate interior of a plant cell and the way it reproduces and results in the formation of a multicellular plant body. The subsequent chapters on tissue, apical meristems, and tissue system give an idea of the ontogeny of plant body *i.e.*, how the cells form tissues, and the tissues, together constitute the system, and how such a developmental pattern helps the plant body to perform the diverse functions that are vital for its maintenance Before passing on to the consideration of the internal morphology of plant organs like roots, stems, and leaves, it has been thought proper to devote separate chapters to important tissues like xylem, phloem, cambium, and periderm. After going through these chapters the student is fully equipped with fundamentals of plant anatomy and is in a position to understand the internal structure of the various plant organs.

The last chapter on ecological anatomy has been written with great care and is profusely illustrated with examples and figures. It alone includes eighty figures and detailed descriptions of more than fifty specimens so as to give an idea of variations in the internal set-up on plants. Detailed descriptions of important stems with anomalous internal organisation have also been included in this chapter.

[illegible] and the [illegible] d recent [illegible]. Some recent works in this direction have also been incorporated so as to give an up-to-date information to the reader.

Comprehensive bibliography has been compiled and added at the end of the book. It is by no means a complete bibliography, but incorporates most of the old and recent publications in the field of plant anatomy and morphogenesis.

The book has been written in a simple and a lucid style. It is not an original work, but it is an attempt to compile available information on the subject so as to make it useful to the students in the colleges and the universities. The author has freely drawn upon the various research journals and eminent works of authors all over the world, and is indebted to the editors, publishers and the authors of those publications.

The author owes his sincerest thanks to his publishers : Messrs. S. Nagin & Co., for their continued help and co-operation in bringing out this book.

Useful suggestions and healthy criticism to improve the book will be welcomed and thankfully acknowledged.

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Dated 17.6.68

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Govt. College
Chandigarh

P. C. Vasishta

CONTENTS

1

INTRODUCTION

THE PLANT BODY AND ITS GROWTH

Plant world simulates gigantic kaleidoscope displaying varying

The vascular plants

types of tissues (see

ultimately grow into a fullfledged plant. This zygote simulates a genetically determined metabolic machine that is geared into action by exogenous chemical substances that determine its operation. These are the growth factors and it is still to be understood as to how they act.

cts of differentiation are not

morphological and anatomi-

of plant body are presented

in legitimate details.

In the seed plants the sporophyte develops from the oospore which develops into an embryo that is protected in a structure called the seed The seed contains stored food and develops from the ovule. In the angiosperms, the seed is enclosed within the fruit. The embryo remains dormant in the seed and can develop into a plant after undergoing a period of rest, which varies with plants. The vascular plant which develops from this embryo has a simple plan of construction. The plant body has a root system and a shoot system. The former generally grows down into the soil and functions to absorb water and the minerals from the soil. The latter grows up and bears branches, leaves, flowers and fruits The stem supports the plant and conducts water and food. The leaves are chief organs of photosynthesis and flowers help in reproduction.

DEVELOPMENT OF THE PLANT BODY IN SEED PLANTS

The mightiest plant in the world develops from a single-celled zygote that undergoes division in an already designed pattern to form a structure called *the* **embryo.** The latter is protected by the **seed** and lies dormant in it. The seed germinates under suitable conditions and the embryo resumes growth and develops into a plant. The embryo

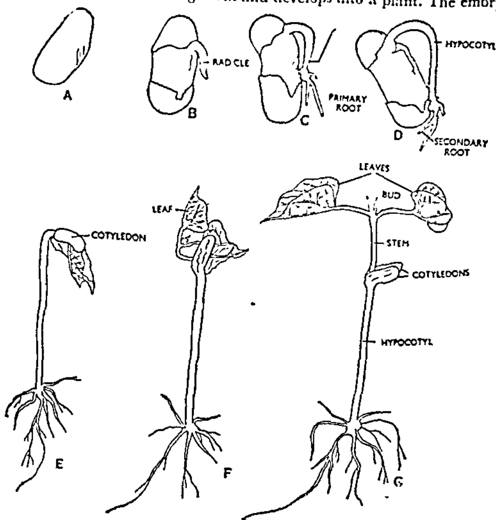


Fig. 1.1. (A—G). Various stages in the germination of the seed leading to the formation of a young seedling (G) with well-developed root. The young stem with first two leaves, and apical bud have also developed (G).

when fully mature consists of three parts. These are : one, two or more cotyledons, also known as seed leaves ; **epicotyl** situated above the cotyledon or cotyledons ... is below the cotyledon or coty... usually called the plumule (emb... the hypocotyl is designated as ra... embryo is a

bipolar structure, containing a young root growing point (radicle) and a shoot growing point (plumule). The **embryo** is surrounded by a

he endospermic seeds. In
in the cotyledons which
rbing endosperm prior to

maturation of the seed. Such cotyledons rarely become leaf-like or photosynthetic. In the endospermic seeds, the cotyledons remain thin and leafy and serve to digest the stored food in the endosperm, and expand into leaf-like photosynthetic organs after completion of this task.

The bipolar embryo undergoes remarkable changes that involve growth by cell division and cell extension, differentiation of new tissues and organs such as roots, stems, leaves and flowers, a series of complicate

patter

ments

Under suitable conditions of germination the embryo is activitated to growth. Its cells absorb water and as a result of hydration the cells in the growing tips are stimulated into mitotic activity. The radicle is

oung root. The
At both the api-
the meristematic
apical meristems.

The resulting new cells undergo elongation and differentiation into new tissues. These tissues give rise to plant organs. The formation of new cells, tissues and organs as a result of the activity of the first formed meristems, constitutes the **primary growth** of the plant. The activity of the meristems brings about the growth in length of the shoot and the root. The tissues and organs differentiated as a result of this primary growth are called the **primary tissues** and **primary organs** and they build up the **primary body** of the plant.

A brief account of the development of the primary body is outlined below :—

The cells formed as a result of meristematic activity in the root and the shoot have a cubical outline and are mu tivacuolate. As a result of absorption of water into th e vacuoles they grow in size and coalesce to form a single big vacuole in the centre. The cell is in an extended condition and has increased in size. The new wall material is synthesized and new cytoplasm and varicus other cell organelles are formed resulting in the permanent increase in the size of cells. This happens in the region of cell elongation in the root and stem tips. The cell elongation is accompanied or sometimes followed by cell differentiation. In the roots, the outer layer of cells either becomes flattened epidermal cells or become root hair cells (in the region of root hair). The root hair cells are those epidermal cells which give rise to tremendously elongated filamentous protuberances that are effective in the absorption of water and minerals. During the formation of the root hair, the nucleus of the epidermal cell generally shifts to the tip of the

lateral protuberance that is destined to form the root hair and appears to be in a great metabolic activity. The root hair develop in great numbers and the cells producing them are short-lived. The root hair producing cells develop in great numbers as the root tip grows downwards through the soil.

The cells in the centre of root differentiate into the vascular elements, as the roots characteristically contain no pith. The core of the central mass of cells differentiates into the **xylem** type of cells. The phloem is differentiated later and both the xylem and the **phloem bundles** are surrounded by the meristematic **pericycle** which gives rise to the branch roots, and entire vascular cylinder is surrounded by the **endodermis**. The radial walls of the endodermal cells develop curious thickenings called the **casparian strips**.

The cells lying between the internal vascular cylinder and the epidermis constitute the **cortex**. These cells are loosely-packed and are parenchymatous in nature with thin walls, distinct nuclei and large central vacuoles. The cells of the cortex generally store food material in the root.

The root grows downwards into the soil through a firm and resistant soil medium and its tip is, therefore, protected by a **root cap**. The cap is made up of a group of cells that are produced by divisions of the meristem and is continuously flaking off and being replaced.

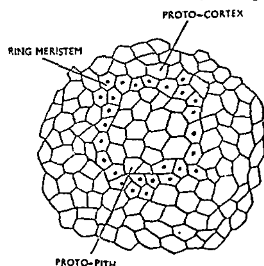


Fig. 1.2. A.T.S. through the shoot apex of *Ranunculus acris* near the apex showing the ring meristem (cells with a dot in the centre) protocortex and protopith (After Helm).

The stem apex like, the root apex, consists of a meristematic zone (0·1—0·05 mm. long) of cells that are in a continuous and a rapid state of division. This is called **promeristem** and has cells with extremely thin walls. Immediately below the promeristem is the **zone of determination** (0·02—0·8 mm. long) which has no visible boundary with the promeristem. In the dicots, this zone has a group of conspicuous cells with dense cytoplasmic contents. These cells in a transverse section are arranged in a circle (Fig. 1.2). It is a remnant of a primordial meristem, which remains behind in a maturing segment, and it retains its activity to divide. Because of its circular appearance it is also called the **ring meristem**. The cells in the centre are the **protopith** and those that are external to the **ring meristem** are the **protocortex** (Fig. 1.2). Posterior to this region

[illegible] ation. In this region the different kinds [illegible] initiated in the **determination zone,** [illegible] The cells of **protocortex** and **protopith** divide and build up the mass of **ground tissue** which has mainly isodiametric cells. The divisions in the **protocortex** and **protopith** are transverse to the longitudinal axis. The cells of the ring meristem divide longitudinally and form elongated cells that mark the position of the future vascular bundles and are known as **procambial strands.** The **protophloem** or the first formed phloem elements differentiate from the procambial elements adjacent to the developing cortex. The protoxylem elements differentiate from the procambial elements next to the pith. In majority of the angiosperms, (dicots) and in the gymnosperms, a layer of procambial cells between the developing primary vascular tissues (xylem and phloem) retains its meristematic activity and functions as the vascular cambium. In some angiosperms (sun-flower, [illegible] places do not [illegible] to ordinary [illegible] and cortex. [illegible] primary medullary rays [illegible] their presence [illegible] *num usitatissimum*, the rays are very narrow and indiscernible and form a continuous primary vascular cylinder. The process of cell differntiation and maturation is much more complex in the stems as compared to the roots because the stem apex has, in addition to stem tissue, to give rise to leaves and buds. The buds arise as minute projections of tissues and, depending upon their structure, develop into vegetative buds or floral buds. In the region of differentiation in the stems, the development of epidermal tissues, the cent [illegible] [illegible] hat [illegible] ow [illegible] ells [illegible] primary cambium.

The account given above gives in a nut-shell the development of the primar [illegible] ons and [illegible] with prim [illegible] cope with [illegible] in the development of a **secondary body**. The process of secondary growth and the formation of secondary tissues will be discussed in the chapters on root and stem.

DIFFERENTIATION

Physiological basis :—Differentiation is one of the most complex unsolved problems of biology. It involves complicated biochemical and biophysical processes whose intricasies we have yet started to understand In the previous pages we have learnt as to how a plant develops from an **oospore** or the fertilised egg. A fully developed plant is only a manifestation of the process of differentiation. It is very difficult to describe or explain the causes underlying this differentiation. The visible morphological changes result from a number of invisible biochemical changes. The anatomical features of a plant only mirror in avisible form the hidden and less obvious physiological events that took place sometimes before

The process of differentiation of tissues, tissue systems and organs follows a distinct and an orderly fashion or a schedule that is already set for a particular species of plant. The organisation of a plant body, its shape and size are determined by certain factors that have not been fully understood. **Polarity** or the plane of cell division is considered to be an important factor in determining the position and shape of the developing organ. Haber (1962) and Haber and Foard (1963) have shown that irradiation of wheat grains prevented nuclear division by preventing synthesis of DNA. In such grains there is no mitosis, but inspite of this the grains germinated and grew into seedlings The leaves developed their characteristic shape despite the prevention of nuclear division. Such seedlings were termed as "**gamma plantlets**" and afford a good material to show that some development can take [illegible] [illegible]on. It indicates that this growth [illegible] primordia already present in the embryo. It appears that the mitosis which look place during the differentiation of the embryo may already have determined the shape and position of the organs present. Cell expansion or cell enlargement also plays a great role in determining the shape of organs. Foard, Haber and Fishman (1965) have demonstrated the enlargement of cells of root pericycle in irradiated wheat seedlings. These cells did not divide, but during their enlargement gave rise to structures the form and position of which simulated lateral root primordia. Such irradiated seedlings showed tissue differentiation and maturation without mitosis. These experiments seem to emphasize the importance of biochemical and biophysical changes that take place during the development of oospore into an embryo. These early changes in which mitosis takes place seem to determine the form, size, shape and position of the future plant. During irradiation experiments either seedlings or mature seeds have been treated, whereas earlier developmental changes had already taken place.

At one stage it was suggested that the level of ploidy (Polyploidy) of the cells might [illegible]. Partanen (1965) is of the opinion [illegible] merely one of the manifestations of [illegible]n or controlling factor. In order to know the initial causes of determination of cell and tissue differentia- [illegible] and development, we must look to chromosomes, genes, and to

some other factors in the cytoplasm. In doing so we should, however, not loose sight of the fact that the genome in itself is dependent upon environmetal control (Grobstein, 1966).

Developmental Pathways. A living cell is capable of following a number of different developmental patterns. Some internal stimulus or mechanism develops and selects one of these patterns or pathways and induces the cell to follow it. Like this the cells follow a particular sequence of development and their fate is determined. This capacity to react to a particular internal or external stimulus in a cell is called **competency**. This competency is attained due to the synthesis of certain messengers in the cytoplasm. Certain regulating devices also develop within the cytoplasm and induce the **competent cell** to follow a particular path of development (Heslop Harrison, 1967). These regulating devices may be certain hormones and other chemicals, which act and determine the future developmental pattern. It has been ascertained, that in plants, a type of balance between several such substances determines the future developmental pattern of an undifferentiated cell. It has been found out that balance between the concentrations of auxin and sugar is important in controlling the differentiation of xylem or phloem from cells which can give rise to either. The competency of a cell and its potentiality to react to various stimuli that determine its future course of development may be retained for long periods. In *Cereus giganteus* it is retained throughout the 100 or 150 years of its life (Popham, R.A. 1958).

Polarity. It is defined as setting up of a structural or physiological difference, between one end of the cell or an organ and the other. For example, the cells in the embryos of *Capsella bursa-pastoris* and cotton show polarised distribution of cytoplasm. It has been observed under the electron microscope that the cells have a large vacuole and scanty cytoplasm at one end and dense cytoplasmic contents at the other end (W.A. Jensen, 1964, 1968). The establishment of polarity is very important in the zygote and is to a greater extent controlled by the environment in which the zygote develops Polarity is considered either to control further differentiation of a cell or a tissue or it is the early manifestation of differentiation. Polarity of a cell may be determined by the nuclear division because the development of nuclear spindle causes disturbance of cytoplasm at one end of the cell. As a result a metabolic gradient is established in the cell and results in polarity. In some cases polarity is established even before nuclear division. Commoner and Zucker (1953) have shown that polarity is established as a result of segregation of specific biochemical systems within the single parent cell. This segregation becomes finalised by laying down of a cell wall between two sister cells. This leads to cellular differentiation. Establishment of polarity may lead to unequal division of the cell (*e.g.* zygotes in ferns) and to a different fate for the two daughter cells formed as a consequence of that division. Such unequal divisions in the zygotes of many plants are very important in the differentiation of various parts of the embryo *e.g.*, the larger cell in the zygote of *Marselia* gives rise to the stem and the leaf of the embryo and the

smaller cell to the root and the foot. Another example may be cited, the mother cell of the stoma divides by an unequal division into a smaller cell with dense cytoplasmic contents and a larger cell with less activity. The small cell acts as guard cell mother cell and forms the two guard cells of the stoma During the development of root hair the epidermal cell divides into a smaller cell with denser cytoplasmic contents and a larger cell The smaller cell shows greater activity and acts as root hair initial whereas the larger cell acts as the ordinary epidermal cell. This unequal or assymatrical division of these cells is preceeded by various differences in enzyme distribution, nucleolar size, etc Polarity is thus the basic cause leading to differentiation.

Distribution of Differentiated Regions. As has already been pointed out the cells are capable of following different paths of development. These cells establish polarity and then develop into various kinds of tissues. These various types of tissues or differentiated regions or structures develop at appreciable distances from each other and form distinct patterns or arrangements. The primary apical meristems, **protoderm, ground meristem,** and the **procambial strands** have a definite arrangement and position. The primary permanent tissues which arise from them have likewise a distinct
in, or from these tissues also
ie stomata that arise from
ment and maintain a certain
distance from each other. The cells of epidermis which give rise to these structures are called **meristemoids.** These meristemoids exhibit a sort of incompatability which is responsible for the establishment and maintenance of distinct patterns of structures that develop from them. Meristemoids of one kind can inhibit the development of their own kind as well as of meristemoids of different destiny *e.g.*, the stomata can inhibit the development of other stomata near it as well as of hairs. This leads to the development of ordinary cells between the meristemoids and thus they become separated from each other by inactive regions. When the meristemoids become inactive, new ones can develop from the inactive regions which separate the earlier ones. This incompatibility among the meristemoids may result from either of the two causes :—
(*i*) competition for substances necessa
and (*ii*) the production of growth
growth. The inhibitory field may in
than those occupied by the meristemoid itself.

Relationship between Tissues. It has been observed that a distinct relationship exists between various tissues and the structures that develop from these tissues. Two examples can be cited :—(*i*) In the leaves of sun-flower (*Helianthus*) the distribution of epidermal cells producing hair depends upon the pattern of underlying vascular tissue that forms the veins. (*ii*) In the leaf of *Nymphaea alba* the growth and development of sclereids in the mesophyll and the stomata in the epidermis are interrelated, because the sclereids never occur below the
Similarly the passage cells in the endodermis of roots of
ocots always develop opposite the protoxylem groups of the xylem

bundles. These relationships of development are clearly visible to us, but their underlying physiological causes or relationships between the various cells and tissues is not completely understood.

Position of a Cell in Relation to other Tissues The importance of position of a particular cell in relation to other tissues is manifested by certain aspects of differentiation in *Monstera deliciosa.* In this plant unequal division ot cells takes place in various tissues. In epidermis the smaller cells develop into hairs. In the hypodermis the smaller cells differentiate and do not develop into any structure and only alternate with longer cells. In the cortex, the short cells develop into **trichosclereids** (Bloch, 1965). This example shows the importance of position of a short cell or the environment of this cell that control its differentiation.

Environmental Aspect of Differentiation. Many experiments have been performed to show that the fate of a cell can be changed by changing its environmental factors. Tissue culture experiments are most important in this respect. A few examples will be cited here to prove this aspect :—

Steward and his co-workers worked on carrot (*Daucus carota*). They obtained small pieces from the secondary phloem of carrot roots. They placed these pieces of tissue in a liquid culture medium under aspetic conditions. They also added coconut milk to the liquid medium. The pieces of phloem tissue began to grow actively and produced a callus like structure. This callus was later transferred to special culture flasks containing liquid medium with coconut milk. The flasks were shaken. As a result some single cells or even small groups of cells saparated from the callus. These detached cells were latter grown separately in separate flasks containing the same medium. These detached cells formed embryo like structures and developed small roots. If these embryo-like structures are transferred to solidified agar agar medium, small shoots also developed opposite the roots. These small plantlets could be grown into fullfledged plants that produced flowers and viable seeds. Such experiments have also been performed on rice, sugar cane, cotton and many other plants with great success. These test tube plants can be removed and even grown outside in the fields. The detached cells of the callus have been seen to behave differently, if we alter the chemical composition of the liquid medium. In this experiment ordinary cells of the carrot root have been made to act like zygotes, if supplied with suitable nutrients. In another experiment, the embryos of wild carrot were removed and culture under aseptic conditions. The embryos proliferated and, when shaken in culture flasks, they detached into separate cells. These detached cells of the

These experiments indicate that ordinary cells of the plant and also cells from embryos can behave like a zygote and later mature into a fullfledged plants. A fully differentiated carrot cell thus retains the potentialities for growth and differentiation, that are normally present

only in the zygote. When removed from the normal plant, each such cell can grow into a fullfledged plant. But when present in the plant, it cannot do so. The position of this cell within the plant or in other words its environments within the plant impose certain restrictions on its development *e.g.*, the phloem cells in the plant will not grow into a complete plant, but will produce phloem tissue alone. On the other hand when these phloem cells are removed from the plant and grown in a free environment containing all the nutrients, it grows into a fullfledged plant. This shows that environment of a cell plays a great role in its future course of differentiation and development.

Genetic Aspect of Differentiation. Genetics or the genes are responsible for many facets of development of a particular individual (plant or an animal). Rather the individuality of every species is due to the genes. A sunflower plant will produce seeds that will develop into sunflower plants alone. This is all due to the action of genes that are carriers of hereditary potentialities of all living individuals. The zygote has all the genetic information concerning a particular plant. *It has to follow a particular course of development to give rise* to an embryo. All the cells of the embryo have the same genetic complement as the zygote, because they are formed by its division. The genes have an appreciable control over the pattern of differentiation to be followed by a cell, but not the overall control. A cell is capable of following several pathways of development, but it has to follow one out of them. This selection of path of differentiation is determined by a certain gene controlled action.

It must be remembered that all the cells of a plant may have the same genetic complement but all the genes cannot come to play at the same time in any cell. As an example, it may be cited that the genes which control the development of flowers will come into play only when [illegible] During vegetative growth these [illegible] me active at the time of flowering [illegible] n a mechanism of their switching on into action by a particular trigger mechanism. The nature of the agents that can trigger this sequential activation of genes, and their action are consequently the keys to the control of tissue and organ differentiation. It is known that certain hormones can control gene action, and histones are also important in this respect. Bonner (1965) puts it, "Small molecules, the hormones for example, turn off or on individual or whole sets of genes in appropriate cells of higher organisms eliciting the production of characteristic enzyme molecules and, in appropriate instances, setting a cell or cells on a new pathway of development." Stange (1965) considered the differential synthesis of enzymes to be the basic process of cell differentiation. It is now known that concentration of particular enzymes often precede the morphological differentiation of certain cells and tissues.

It appears that some complicated interactions between the genetic complex, the biochemical and biophysical reactions within the cells and the structural features of the entire plant are involved in the determination of differentiation patterns.

2

THE CELL

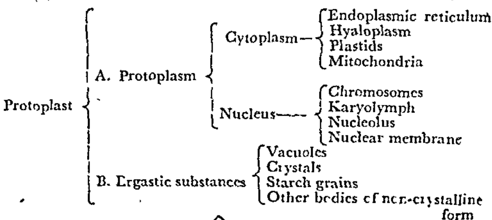
In the words of Sir Rudolf Peters (1968), "The living cell is the most important invention in nature. In its capacity to maintain the constant equilibrium in which life is manifest, it must be the continuous wonder of any thoughtful person".

Definition. The biologists have, for more than a century, agreed that the cells are the basic structural and functional units that make up a plant body or an animal body. It the unicellular plants, the cell itself is the organism. *A plant cell may be defined as microcosm having a definite boundary or the cell-wall within which complicated chemical reactions are going on. A cell devoid of this chemical action is inert and is considered to be a dead cell.* The seat of this chemical activity is the protoplasm enclosing in it a denser body called the nucleus.

Size and shape. The cells vary greatly in sizes and shapes. The size of the cell varies from the bacterial cells that measure less than a micron in diameter to the 1—3 millimetre long cells of some fibres. The cells of viruses are still smaller and can be seen only under the electron microscope and, on the other hand, some fibrous cells grow to a length of 20—550 mm. (fibre cells of *flax*, *hemp* and *rhea*). A cell taken from an elongating zone of root or stem tip is a box-like structure measuring about 50μ long, 20μ broad and about 10μ deep. It has an approximate volume of $10,000\mu^3$. The shape of the cells also varies. It may be rounded, polygonal, oval, rectangular, cylindrical, ellipsoidal and in some cases very much elongated.

CELL STRUCTURE

A plant cell is composed of two major parts :—(i) The **protoplast** and (*ii*) **cell wall.** These can further be sub-divided as follows :—



A brief discussion of the various parts of the protoplast is given in this chapter.

The protoplast is a common term for all the living and non-living components of the cell. These components include the protoplasm and the ergastic substances.

A. PROTOPLASM

It is the essential living component of the protoplast. It is the only substance that has the unique property called the life and the cells possessing it are considered to be living and those lacking it are dead. It is an illusive substance with dramatic properties, that have baffled the biologists for centuries and it is yet beyond the scope of the biologists to make a living protoplasm. Huxley has aptly described it as a *physical basis of life.* It has been a subject of detailed research for the last many years and with the incoming of electron microscope much has been added to our knowledge of the structure of the protoplasm and its constituents. The biochemists have brought into light the submicroscopic structure of protoplasm *i. e.*, the molecular pattern of protoplasm. Protoplasm is the seat of numerous complicated chemical and other cellular processes *e.g.*, osmosis, nutrition, metabolism, growth, respiration, reproduction etc. All these functions are performed by a number of living constituents of the protoplasm. Two major parts into which the protoplasm is usually divided are the **cytoplasm** and the **nucleus** (Fig. 2.1). Each one of these two parts has been revealed to possess a complicated structure and to possess several living bodies having specific functions All these structures are specialised masses of protoplasm that have been differentiated into distinct bodies to perform specialised functions. A brief account of all these living inclusions will be given in the subsequent pages. The protoplasm is bounded by a living membrane called the cell membrane.

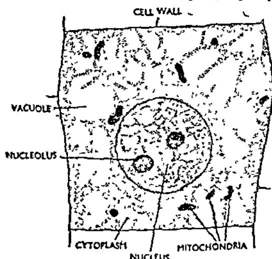


Fig. 2.1. Various parts of a plant cell as seen under the light microscope.

Cell membrane (Figs. 2.2—2.4). All the cells, whether of the plants or animals posses [illegible] protoplasm called the plasma membr[illegible] s a living constituent of the cell. [illegible] in possessing an additional non-living cell wall external to the plasma membrane. It is now universally agreed that the plasma membrane forms boundary of all the living cells but not much is known about its [illegible]ture. It has a very important role in the life of a cell and acts as

a screen through which all substances that enter or leave the cell must

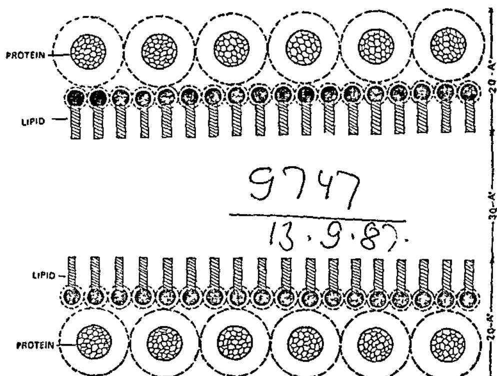


Fig. 2.2. It illustrates the structure of plasma membrane. The globular protein is shown much enlarged (After *Davson* and *Danielli*).

pass. It is elastic in some cells and rigid and unyielding in others and is capable of repair, to a limited extent, if punctured by a needle. It is also considered to be able to grow along with the enlargement of the cell. The cell membrane, as viewed under the electron microscope, is seen to be double-layered and punctured by numerous pores. Regarding its chemical composition it is believed that a double layer of lipid

... sandwich model ...

including surface tension and thickness estimates (Fig. 2.2).

In the year 1938 Harvey Danielli proposed a model that ... membrane is **bimolecular lipid leaflet** ... s view came later ... e micrographs of the cell-membrane portrayed it to consist of an outer and inner dark (Osmiophilic) layer. These two layers were separated by a high (Osmophobic) layer at high magnification. The clear area measures about 30A° thick (Fig. 2.2), and each dark layer measures about 25A° thick. This model corresponds to the sandwich model. This trilaminar pattern of cell membrane structure led Robertson (1959) to propose the concept of a **"unit" membrane** (Fig. 2.3) with a trilaminar appearance. This unit membrane has been found to be

characteristic of both the outer and inner membranes of chloroplasts, mitochondria, endoplasmic reticulum, nucleus, Golgi complex, and

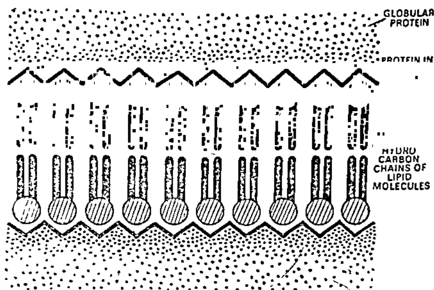
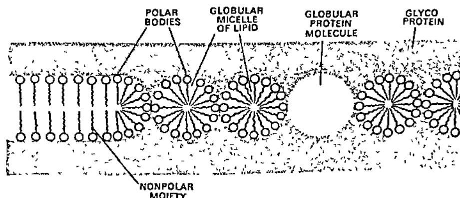


Fig. 2.3. A classical model of plasma membrane structure as proposed by *Robertson* (1959).

lysosomes. Thickness of the membrane may vary in the same cell or in various cells from 15—100Å.



[illegible] membrane in which globular [illegible] bimolecular leaflet [illegible] of the lipid layer. [illegible] igrammatic fashion. Only a polar group (Ó) and a non-polar moiety are shown. One globular micelle of lipid has been replaced by globular protein molecule. (After *Lucy J. A.*)

Lucy (1964) proposed another hypothetical model (Fig. 2.4) called the **micellar model** and is based on the concept that a micelle is a colloidal aggregation of molecules. In this micellar model for natural

membranes, the *globular lipid micelles* can be in *dynamic equilibrium* with the bimolecular leaflet structure. It is evident from Fig. 2.4, which portrays a transverse section of the m

rane. It has a power of selectivity and allows some molecules to pass through it and not others. Such a membrane is known as **differentially permeable** membrane. Cell membranes are permeable to O_2, and CO_2, water molecules, aminoacids, glucose, potassium, etc., whereas molecules of sodium cannot pass through them. The diffusion of water in or out of the cells depends upon whether the solutions exterior to the cells are hypotonic or hypertonic. Similarly, exchange
concentration out of the cell and inside
permeability of the cell membrane is not
but is subject to change from one moment to the other. This property of selective permeability is dependent upon the structure of the cell membrane, size and nature of the entering molecules and to some extent the cell also determines the behaviour of the membrane. The question as to how the cell controls the behaviour of membrane is not answerable as yet. The substances that enter the cell membrane by diffusion must be dissolved in water or they must be soluble in the components of the cell membrane. Sometimes, pinocytotic invaginations of plasma membranes have been noticed in *Elodea canadensis* (Fig. 2.12) and in the guards of stomata of many plants (see James and Hilton, 1972). These invaginations in the guard cells have been considered as artifacts that occur during processing (Fowke and Setterfield, 1969). Huang, J.S. Huang, Pi-Yu and Goodman, R.N. (1973) extracted structural proteins and lipids from thylakoid membranes of *Nicotiana* chloroplasts and dissolved them separately in sodium dodecyle sulphate. The dissolved proteins aggregated into spherical clumps, and lipids into globules composed of alternating light and dark bands upon dialysis against dilute beta-buffer containing 20m M Mg^{++}. The reaggregates of the mixture of structural proteins and lipids formed membranous structure. The appearance and thickness of these reconstituted membranes *were similar to those of thylakoid membranes prepared from* sonicated chloroplasts.

CYTOPLASM. It is also known as the cell protoplasm and is the protoplasmic mass of the cell leaving aside the **nucleus**. Its surface layer is the plasma membrane or the cell membrane or the **ectoplasm**. The mass of cytoplasm inner to the plasma membrane is known as **endoplasm.** Cytoplasm is the main assembly line of the cell and its output is either to produce the various secretions, storage materials, pigments or even the new cells, or to help in the transmission of CO_2 and O_2, transmission of messages, protection and movements. In order to perform all these functions, the cytoplasm requires the necessary raw materials, energy, machinery necsssary to do the job, and the ways and means to distribute the products of service. The plasma membrane

helps in the passage of raw materials from the outside environment. The necessary energy required to convert these raw materials (H_2O and CO_2) into the building material of the protoplasm is obtained



Fig. 2.5. Structure of plant cell as seen under the electron microscope.

directly from the sun. This is true of the plant cells only. This in-take of the solar energy occurs in the plants during the process of photosynthesis and the chloroplasts which contain the chlorophyll are the chief structures that absorb the radiant energy of the sun. They transform the radiant energy of the sun into chemical energy which the cell can use as it needs. This process requires lot of chemical activity and a chain of reactions accelerated by a battery of enzymes are involved in it. The chemical energy stored in this cell is made available in a usable form to the cell by the curious and very important structures called the **mitochondria**. Both these structures that are present in the cytoplasm provide the necessary machinery to do its job. In addition to these two important constituents of the cytoplasm, there are other living parts, such as **golgi bodies, ribosomes,** and the **endoplasmic reticulum** (Fig. 2.5).

The cytoplasm in the young cells completely fills up the space between the nucleus and the cell wall (Fig. 2.1.). As the cell grows in size the cytoplasm shows the appearance of numerous cavities of variable sizes and shapes that are protoplasmic and are called the **vacuoles** (Fig. 2.6 A). Continuous growth of the cell results in the fusion of numerous smaller vacuoles to form bigger vacuoles. In the mature cells, all the vacuoles fuse together to form a large central vacuole (Fig 2.6D). The cytoplasm in such cells is generally in the form of a thin layer applied to the inner surface of the cell-wall. The nucleus and the other structures lie embedded in the layer of cytoplasm. In some cases, the nucleus is suspended in the centre by a number of cytoplasmic strands that radiate out from a mass of cytoplasm surrounding the nucleus. The strands divide the big central vacuole into a number of smaller vacuoles.

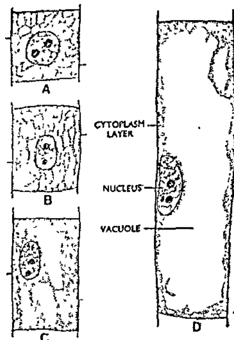


Fig. 2.6. (A—D). Various stages in the growth of cell and appearance of vacuoles. A. Numerous small vacuoles. B—C, Vacuoles coalese to form bigger ones D. Big central vacuole with nucleus embedded in the lining layer of cytoplasm

Endoplasmic Reticulum (Fig. 2.7). The cytoplasm as revealed by the electron microscope is as structurally compartmentalised as are the larger cellular bodies like the nucleus and the mitochondria. It is semiviscous fluid that is densely traversed by a highly ordred arrangement of membranes that form an **endoplasmic reticulum** or the **ergastoplasm** (Fig. 2.5). The recent evidence suggests

that the endoplasmic reticulum is a network of tubes extending througout the cytoplasm. Some of these tubes seem to open on the cell-membrane and are thus considered to be in direct contact with the fluids surrounding the cell. They also seem to be in contact with nuclear membrane (Fig. 2.5).

The endoplasmic reticulum is believed to occur in two forms, rough (granular) and smooth (agranular). The former are studded with ribosomes whereas the latter are without ribosomes. There is a continuity between the two forms, but they seem to differ in certain respects *e.g.*, only the granular endoplasmic membranes are in confluence with the outer nuclear membrane The agranular membranes are instead connected with the golgi complex. The granular form is associated with protein synthesis whereas non-granuler or smooth endoplasmic reticulum is associated with non-protein synthesis. The agranular or non-granular type has been related to lipid and chlorestrol metabolism.

The functions of the endoplasmic reticulum can be listed as belows .—

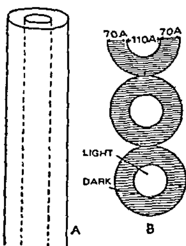


Fig. 2.6 A. It illustrates the structure of a microtubule A, Microtubule as seen from one end. B, Detailed structure of a part of wall of microtubule.

(*i*) It forms a transport system for the proteins.

(*ii*) It plays some role in wall formation Northcote. 1963). It determines the plane of cell division.

(*iii*) The membranes of endoplasmic reticulum possess osmotic properties and thus help in regulating the entry and exit of materials into and out of the interior.

(*iv*) It helps in the synthesis of lipids (Siekevitz, 1963, 1965)

(*v*) It helps in glycogen systhesis (Coimbras and Leblond, 1966).

(*vi*) Formation of exine patterns in pollen grains and determination of sites of germ pores in exine is determined by the prior deposition of endoplasmic reticulum Heslop-Harrison, 1966). The development of pores in nuclear membrane and of sieve pores in sieve plates are also attributed to the prior deposition of endoplasmic reticulum at such places (Esau, 1962 ; Heslop-Harrison, 1966).

(*vii*) The abstriction of vesicles from the golgi complex (dictyosomes) is attributed to be due to a role played by the endoplasmic reticulum. (Heslop-Harrison, 1966).

The ground substance lying between the tubules of endoplasmic reticulum is called **hyaloplasm**. It appears to be structureless under the ultramicroscope and may contain scattered ribosomes and microtubules.

Microtubules (Fig. 2.6A). Ledbetter and Porter (1963) demonstrated the presence of fine elongated tubes in the peripheral cytoplasm of about all plant and animal cells and even in bacteria. In plants they are more frequently seen around the periphery of meristematic cells. These are usually found attached to the plasmalemma and are regarded to be responsible for the orientation of cellulose synthesis. They are very clear during the mitotic cell division as cytoplasmic fibrils. They are several microns in length and vary in diameter from 150Å to 250Å with a wall thickness of about 60Å. They are regarded by some authors to be fibres of the spindle apparatus. They are mostly made up of protein. The various functions attributed to them include : (*i*) They are skeletal in nature , (*ii*) they are regarded as contractile and thus concerned with cytoplasmic movements , (*iii*) they are considered to be connected in some way with cell-wall formation and growth ; (*iv*) some researchers consider them to be the components of the spindle.

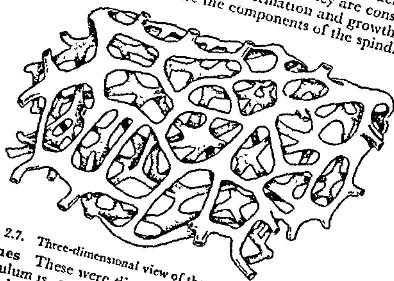


Fig. 2.7. Three-dimensional view of the endoplasmic reticulum.

Ribosomes These were discovered by Palade in 1953. The endoplasmic reticulum is coated with numerous tiny granules (Fig. 2.5). Their extremely minute size may give an impression of their being unimportant structures, but they are now certainly known to have a major role to play in the cell. These tiny granules are known as **ribosomes.** The ribosomes appear opaque bodies measuring 150Å in diameter, under the electron microscope. They do not possess the power to multiply themselves and originate within the nucleus. They derive their name because they are known to be composed largely of ribonucleic acid or RNA. They also contain protein. The RNA constitute 40 to 60% of the dry weight. Each ribosome is an aggregation of two subunits which are held together by bonds which appear to need magnesium ions for their continued stability.

In bacteria, the ribosomes have been found to possess a sedimention coefficient (=Svedberg unit) of the 70 S type. It is composed of two sub-units, one 30 S and the other 50 S. During protein synthesis *t* RNA and *m* RNA bind to the 30 S sub-unit. The growing polypeptide

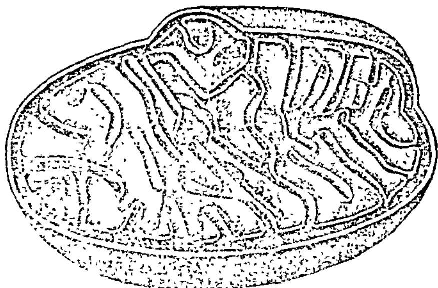


Plate 1 Crista type of Mitochondrion.

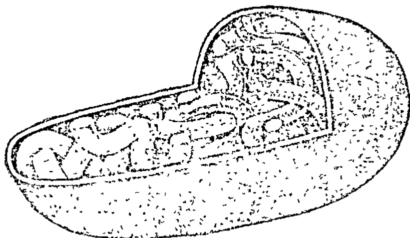


Plate 2. Tubular type of Mitochondrion.

organism. They also enable a developing organism to remove structures no longer in use, for example, cells in the tail of a metamorphosing tadpole. They also digest engulfed food particles and living bodies that enter the organism through pinocytosis. The origin of lysosomes is poorly understood but there is evidence to indicate a developmental sequence. They appear as **pre-lysosomes** whose enzymes do not engage in hydrolytic events. The next stage is of the **lysosomes** which [illegible] tion has occurred. [illegible] st their enzymes [illegible] are formed in a golgi complex. Another view is that they are formed from endoplasmic reticulum. It is also believed that they arise from **autophagic vacuoles.**

Another belief is that acid hydrolases occur freely in the cytoplasm before becoming concentrated within the lysosomes. Some evidence

Plate 3 Golgi bodies with released vesicles.

Plate 4. Sectional view of a chloroplast.

also exists that substances are engulfed by a cell through the action of **endocytosis** (this process is called heterophagy) thereby forming a **phagosome** (Fig. 2.8), which is regarded as the prelysosome. After

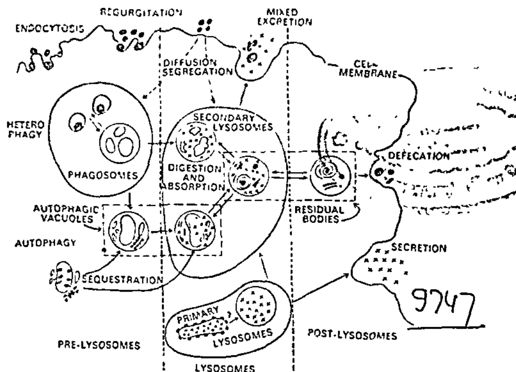


Fig. 2.8. It illustrates the various forms of lysosomes and related particles and the different types of interactions which they may exhibit with each other and with the cell membrane. Acid hydrolases are represented by crosses. (After *de Daure, 1966*).

lysosomal enzymes have digested the substances, the entity forms a residual body containing undigested debris The debris which is the lipid is ejected from the cell by **exocytosis**. Autophagy or formation of **autophagic vacuoles** takes place within the cytoplasm. It follows a similar route (same as heterophagy) of degradation.

Mitochondria (Figs. 2.9 and 2.10). They are found in most of the plant and animal cells (blue green algae and the human red blood cells are exceptions) and are considered to be the "power houses" of the cell. It is now known with certainty that these bodies are responsible for much of the energy-producing activity of the cell. They are also responsible for other important processes of metabolism, such as fat synthesis.

They range in size from 0·2 to several microns in length and in shape from spherical to rod-shaped or sausage-shaped structures.

but in some algae there is only one mitochodrion. In some cases, their number may go up to 1000.

Each mitochondrium is enveloped in a double-layered membrane made up of lipo-protein. These two membranes are separated by a space containing somewhat of fluid matrix. The space is about 80—100A° wide. The inner membrane is convoluted into numerous plate-like structures, called the **cristae** (Fig. 2.10). These are called **cristae type of mitochondria.** The cristae are always shorter in mitochondria of plant origin than in those of animal cells and are sensitive to changes in the medium. The cristae provide great surface area in the interior of the mitochondrion. Matrix granules, about 300-500A° in diameter, may be found in the intercristal spaces. These have been identified as insoluble inorganic salts. The outer membrane is quite elastic and can be stretched to 100 times its normal dimensions. So a mitochondrion can diminish or increase in size and there is some evidence to suggest that this variation in the increase or decrease in the size of the mitochondrion can bring about variations in its activities. Inside the inner membrane of a mitochondrion is a viscous region known as the **matrix.** The citric acid cycle enzymes as well as others are located there Ribosomes are scattered as small granules in the matrix of the mitochondrion.

Mitochondrial origin has been studied in *vivo.* They multiply by fragmentation of the pre-existing mitochondrion. In some algal cells, where there is only one mitochondrion, it divides only with the nucleus, whereas in cells with numerous mitochondria they are distributed randomly during mitosis. After the completion of nuclear division and wall formation the mitochondria may increase in size and then fragment or divide to form new mitochondria. This division takes place either by the formation of a dividing membrane or by constriction and subsequent separation across the narrow neck. It has been suggested, based on electron micrograph studies, that mitochondrial formation is an important activity of the interphase nucleus. In this case the inner nuclear membrane invaginates at specialised regions to form intranuclear mitochondria, which are later extruded into the cytoplasm. They are also formed by the budding of nuclear membrane. The bud protrudes out into the cytoplasm and later on separates as a small initial of mitochondrion. The existing mitochondria may also produce such initials by budding of their membrane. These initials may also appear *de novo.*

Regarding the functioning of the mitochondria, they perform two important tasks. The first is that through a series of enzyme-controlled ... proteins and fats into smaller molecules ... These reactions ... ult of oxidation is not dissipated as heat but is passed on to other molecules that contain phosphate (PO_4) where it is stored by a process of phosphorylation in the form of high-energy phosphate bonds. The principal molecule which energy is stored is adenosine triphosphate or ATP. The ...nd task performed by the mitochondria is that they secrete this

molecule of ATP in the cytoplasm where energy is needed. The typical cell contains hundreds of these mitochondria that are distributed throughout the cytoplasm where they actively secrete biological energy. So a mitochondrion can aptly be regarded as the "Power house of the cell." It provides the cell with most of its usable energy.

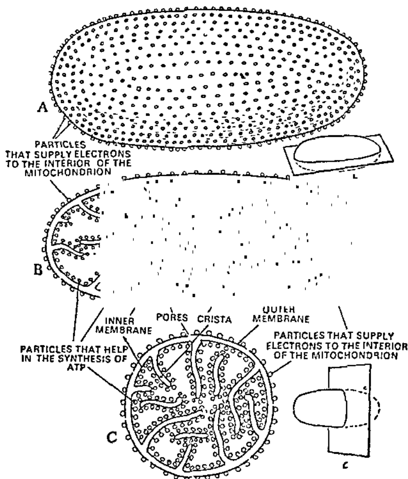


Fig. 2.9. (A—C). Ultra structure of a mitochondrion.
A; Mitochondrion as seen in surface view.
B; Mitochondrion as seen in a section passing in horizontal direction.
C; Mitochondrion as seen in transection.

[illegible] ...netic DNA, make their own [illegible] the mitochondrial DNA is [illegible] In mammalian cells [illegible] of 11 × 10[illegible]. There [illegible] an evidence that mitochondria contain ribosomes, tRNA and activating enzymes. The general conclusion is that they can synthesize protein in a living cell, but it does not have the capacity to [illegible] any specific mitochondrial protein. They are dependent on [illegible] for needed structural metabolites e.g. building blocks of DNA [illegible]

and enzyme making. They arise by division of pre-existing mitochondria and live as symbionts in the cells of higher organisms Lipids, proteins and sulphur particles have also been reported from the mitochondria (Lehninger, 1965). The electron transport bodies (ETB) present on the inner membrane are tennis racket-like bodies having a foot embedded in the membrane, a stalk or the pedicel which is 35—50Å long and head, that is 70-100Å in diameter(Parsons, 1963). These

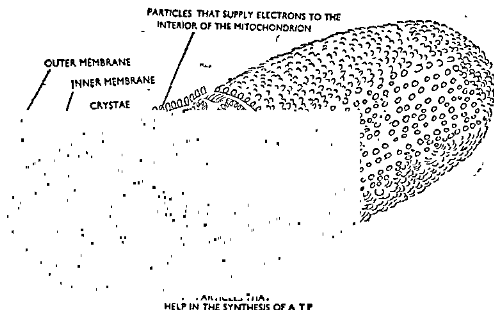


Fig. 2.10. Structure of a mitochondrion as seen under the electron microscope.

bodies appear to be actively involved in phosphorylation accompanying respiration. Joachim Bogen (1968) reported a different type of mitochondrion in the flagellates *e.g. Paramecium.* In this type there are no cristae but long sausage-shaped tubular outgrowths arise from the inner membrane and twist around each other to fill the mitochondrion. These are called **tubular type** mitochondria and are known only in unicellular animals. In some plants, he reported a third type called the **saccullus type** because in them the outgrowths are sac-like.

Cytological evidences from a number of plant and animal cells suggest that calcium is involved in the structural organisation of mitochondria. Jones and Lunt (1967), Bushneva and Somikhatova (1965, pp 106-112) studied the effect of calcium deficiency on the mitochondria of pea seedlings and observed that it causes the swelling of cristae which retar

G

ous group of membranous e usually bladder-like membranes that occur widely ing plant and animal cells. These were first recognised by Golgi in 1898 in nerve cells of the barn owl. The Golgi bodies have, however, been regarded as rich in fatty

materials and they readily stain black, when treated with osmium or silver stains. They consist of a series of double membrane bounded spaces, stacked one upon the other like a pile of saucers and giving rise to membrane bounded blebs or vesicles at their margins These vesicles have a diameter of 400-800 A° and when fully distended break away from the terminal expansions of the cisternae. The golgi membranes are smooth and appear 60A° thick. It has been hypothesized that there is a continuity of the membranes forming the nuclear outer membrane, the endoplasmic reticulum and the golgi apparatus. This continuity of the membrane system has led to the membrane flow hypothesis. Such a flow would account for rapid transport through the endoplasmic reticulum and the golgi complex spaces. There are evidences against such a hypothesis which indicated that the cavities of golgi complex are not continuous with the lumen of the endoplasmic reticulum. Such an evidence indicates that transport of newly formed proteins in the endoplasmic reticulum is effected by vesicles budded off from the reticulum and these smooth surfaced vesicles coalesce with golgi membranes thus discharging their contents into golgi vesicles. Their membranes are smooth. The two faces of [illegible] properties indicating a difference [illegible] id outer surfaces (Pollister and [illegible] fic gravity of 1·09 and 1·13, respectively. The membranes contain hypoproteins, lipids, enzymes and even nucleic acids. Some recent studies in plants (earlier stages in the germination of spores in *Malleuccia struthiopteris*) indicate their active appearance in the young dividing cells. The inside of the golgi complex appears to be rather fluid in consistence and has low enzyme content. Lipid globules and protein granules have also been found in the golgi channels (Hodge, 1955). The golgi bodies have been seen to release, vesicular or sac-like bodies called the golgi vesicles. Such vesicles have been seen in some plant cells to travel to the region of the growing cell wall. In some cases, they have been seen along the growing septa in the recently divided cells.



Fig 2 11 A, an amyloplast with a starch grain. B, a leucoplast.

The exact function of the golgi complex is not known. Some speculations are given below :

1. They might be concerned with secreting some substances that aid in the growth of the cell.

2. They are thought to be concerned with the manufacture of certain enzymes that control the regeneration of membrane system throughout the cell.



Fig 2.12 A proplastid with a prolamellar body.

3. They help in the transport of s me important materials.

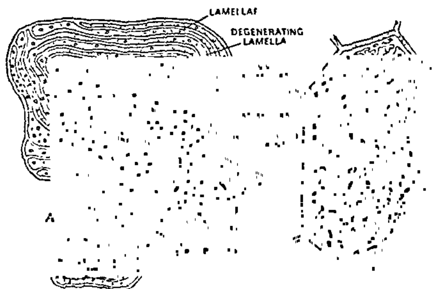


Fig. 2.13. A, Ultrastructure of a chromoplast. B, Chromoplasts as seen under ordinary light microscope.

4. The uptake of monosaccharides occurs in the golgi membranes.

5. They take active part in the synthesis of mucopolysaccharides (Neutra and Le-Blond, 1966).

6. It has been shown that the proteins formed in the ribosomes may travel is a endosplasmic reticulum to the Golgi-bodies and subsequently appear in the pinched off vesicles

7. Very recently, it has been seen that Golgi-bodies convert proteins into glycoproteins.

8. It is also possible that Golgi bodies may be responsible for synthesizing large carbohydrates.

Plastids They are chara... lls alone They are absent ... n algae. Plastids are sp... globular, spherical, or discoid in shape and vary greatly in size. Every plastid is surrounded by a membranous layer which separates them from the remaining cytoplasm. The plasma of plastid, like the nucleus, contains a small amount of nucleic acids. They are living structures that are capable of division and increase in number. The plastids always arise from pre-existing structures, called the proplastids (Fig. 2.12) but the origin of these remains doubtful. It is believed that proplastids are very likely to be found in the 'ribosomal fractions, which can be isolated only after very high speed centrifugation. In sexual reproduction, the proplastids are believed to be carried over from one generation to the next in the gametes. The more recent classification of plastids is :—

(*i*) **Leucoplasts,** which are colourless and photosynthetically inactive.

(*ii*) **Photosynthetically active chromatophores,** which include chloroplasts, phaeoplasts and rhodoplasts.

(*iii*) **Photosynnthetically inactive chromatophores** which include the chromoplasts.

1. **Leucoplasts** (Figs 2.11. B). These are plastids ... colour and are gen... *e.g.*, cells of roots a... parts of the plant that are not exposed to light and in parasitic and saprophytic angiosperms and also in variegated leaves. They are considered to have evolved from green chromatophores as mutations involving loss of chlorophyll They lack the layered structure and the photosynthetic apparatus of the chloroplasts and are of two kinds : the smaller leucoplasts and the larger leucoplasts. The smaller ones can change into large ones or into chloroplasts or the chromoplasts. The larger leucoplasts are known as the **amyloplasts** (Fig. 2.11, A) or starch builders. They possess an elaborate enzymatic machinery necessary to synthesize such materials from smaller precursor molecules.

2. Chrom... , B). They are photosythetically ... harbour a high concentration of ...oid pigments. These bodies a... to the next by means of propla...

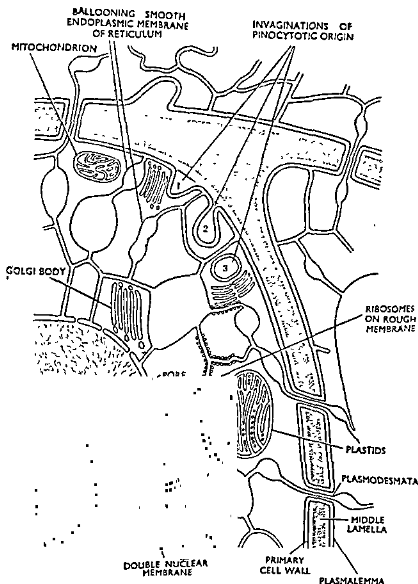


Fig. 2.14. Portion of a plant cell of *Elodea* sp. as seen under electron microscope. Note the invaginations of plasma membrane and ballooning of endoplasimc membrane.

like structures carried in the maternal cytoplasm. They are usually found in the coloured petals of flowers and ripe fruits. The function of the chromoplasts is not clear except that they impart beautiful colouration to the plant parts. The chromoplasts in the petals of *Ranunculus* flower developed first as chloroplasts and then ceased to be photosynthetically active. In *Fucus* (brown alga), the chromoplasts have been seen to possess a double membrane which encloses a matrix (stroma) intersected by rather coarse looking lamellae. Such a structure is revealed by chromoplasts of many higher plants also. It is believed that the pigments of the chromoplasts are present within the colourless

stroma, either in the form of crystals or numerous small grana. The chromoplasts vary in shape and may be spherical, angular, needle-like or even rhomboidal. Their colour is due to the presence of carotins and usually yellow xanthophylls. White flowers contain no pigment. The whiteness is the result of reflection of the white day light by inter-cellular layers of air. In case we remove this layer, the bruised parts become transparent.

3. **Chloroplasts** (Figs. 2.15—2.17). They are the green plastids that are characteristic and unique structures of the green plant cells. They are coloured green due to the presence of a green colouring matter called the chlorophyll. The chlorophyll appears mostly in bodies about ·04μ in diameter, called the **grana**. They are the seat of photo-synthetic activity of the green plant cell. In the higher plants, the chloroplast is a disc-shaped or spherical structure ranging in diameter from 4—10μ by about 1-2μ in width. In the unicellular and multicellular algae, the chloroplasts assume various shapes and have bigger dimensions. The chloroplast, as
transmitted maternally.
type of division process anc
chloroplasts will develop only from
but in the gymnosperms the trans-
loroplasts can be accomplished even in total darkness. The proplastids possess a sort of para-crystalline centre of canals that, under proper stimulation by light, develop into layers.

Structure of Chloroplast. With the invention of electron microscope, the biologists have made tremendous studies on the structure and development of the chloroplasts in a larger number of plants. There is a general agreement that every chloroplast in the vascular plants is bounded by a double-layered, differentially permeable membrane. Each layer of membrane is about 50A° thick. The inner membrane of the chloroplast may invaginate to form the complex internal lamellar system that traverses the stroma. The inner membrane can also form vesicles that coalasce to form lamellae. Weier and Benson (1967) stated that these lamellae are of two types :—

1. The **Fret membranes** that are composed of one layer of sub-units of protein and lipids.

2. The **partition membranes** that are composed of two layers of subunits of lipids surrounded by single layers of subunits of proteins.

The substance of the chloroplast or the **stroma** has been revealed to possess an elaborately bordered structure. The **stroma** is traversed by parallel, double-layered membranous lamellae that run the entire length of the chloroplast. At places these layers become more thickened than their usual cross-sectional dimensions and, when several such layers thicken at the same point, they form **grana** (Fig. 2.15). These thickened lamellae appear disc-shaped and give the appearance of stacks of discoid lamellae or like the piles of coins. There may be 10 to 100 lamellae stacked up to form a granum that varies in diameter from 0·3—1·0μ. These grana are the specialised areas of the chloro-

plast where chlorophyll is found. [illegible] intergranum lamellae which traverse [illegible] may be present in a chloroplast. Sta[illegible] found in the stroma. It is believed that the chlorophyll is spread in monolayers on the layers of the grana, and thus occupy an enormously

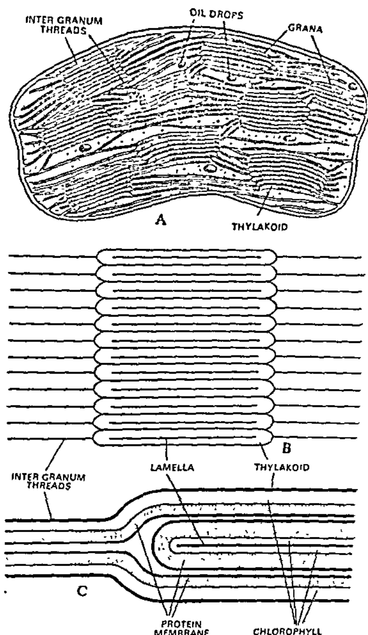


Fig. 2.15. Structure of chloroplast. A, A chloroplast as viewed under electron microscope. B, A granum. C, A thylakoid showing sites of chlorophyll formation.

increased surface area for the trapping of light energy. It is now considered that the *granum* is a structural unit and chlorophyll is evenly distributed in both granal and stromal lamellae.

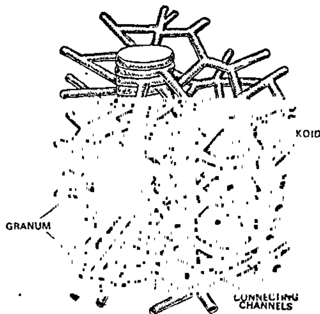


Fig. 2.16. It illustrates the structure of a granum.

After a careful study of the chloroplast structure under the electron microscope, the following points become quite evident :—

1. The entire chloroplast is enclosed by a membrane which is composed of two unit membranes.

2. The envelopes of the chloroplast or the membranes enclose the [illegible] no characteristic struc- [illegible] of microbodies, stroma [illegible] also been reported in the stroma of many chloroplasts.

3. Several big grains called starch grains lie in the stroma.

4. Many lamellae run through the stroma, sometimes, from one end to the other, though quite often they may end blindly.

5. These lamellae are always paired and joined together at the ends, so they look like elongated sacs or cisternae.

6. At certain places the lamellae become flattened and are called **thylakoids.**

7. At certain points the thylakoids have between them still smaller thylakoids and these are usually numerous and look like stacks or piles of coins. These heaps of flattened and circular thylakoids are called the **grana.**

Hohl (1960, 1961) observed for the first time a membrane-bound body in the chloroplasts of *Datura stramonium* and named it as

"Einschlusskorper". Later Stelter and Laetsch (1969) and Boass Laetsch and Price (1972) observed it in *Nic tiana tabacum.* They co sider this body as a storage centre.

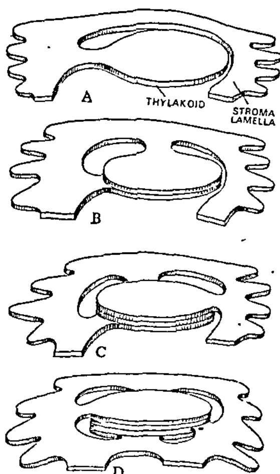


Fig. 2.17. It illustrates the formation of thylakoids as outgrowths of stroma lamellae. The thylakoids are laid one above the other to form a granum. (After Heslop Harrison)

Horner and Bowen (1965) studied the development of chloroplasts in the strobili of *Selaginella* They reported the appearance of spherical bodies called the **thylakoids** on the inner surface of the inner membrane of the chloroplasts. These thylakoids increase in number and come to lie close to each other forming chains. Later on they start flattening and begin to elongate into future grana. Heslop-Harrison (1963) is of the view that a granum consists of a number of flattened discs called the **thylakoids** (Fig. 2.17). These thylakoids arise as marginal outgrowths of a stromal lamella and become superimposed in an orderly manner to form a granum (Fig. 2.17). It means that a granum consisting of varying number of superimposed thylakoid discs arises from a single stromal lamella. According to older workers the grana lamellae

arise by vesiculation and elaboration of inner chloroplast membrane. Others have reported the presence of a pro-lamellar body in the chloroplast. This pro-lamellar body later develops into the lamellae. Stelter and Laetsch (1965) studied the development of lamellae in the developing Tobacco leaves and reported that all the three mechanisms (*i.e.* formation of thylakoids, vesiculation and pro-lamellae body) des- ... ation of lamellae at various ... obacco. They conclude that ... and granal development acting simultaneously in the same system Calvin and Hodge (1959) are of the view that a granum is formed by the infoldings of lamellae. Wettstein (1959) is of the opinion that simple piling of lamellae closed at ends leads to grana formation.

Susalla Anne and Paul Mahlberg (1973) have reported two types of chloroplasts in a green leaf tissue of a genetic albinostrain of Tobacco. These are chloroplasts with or without thylakoids. The chloroplasts with thylakoids are again of three kinds :—

1. Chloroplasts with thylakoids randomly scattered in the stroma. Grana are not evident.

2. Chloroplasts with thylakoids organised into distinct piles forming grana.

3. Chloroplasts with a single giant granum.

Plastids without thylakoids are highly vacuolated to varying degrees. Freeman and Thomas (1970) also reported three morphologically distinct chloroplast types in the developing leaves of *Opuntia basilaris*. These are epidermal cell chloroplasts that contain a **prolamellar body** and a **stroma-centre.** There is very limited granal development ; guard cell chloroplasts that lack stroma-centre at maturity and mesophyll chloroplasts that have microbodies, extensive granal development and no stroma centre at maturity. Stroma-centre is found in the last two types only during early development stages. Phytoferratin bodies were absent in mesophyll chloroplasts but were present in epidermal cell chloroplast. **Stromacentre** is a specialised body composed of fibril material This term was coined by Gunning in 1965 to describe fibril inclusions found in all stages of chloroplast development in the leaves of *Avena.*

... DNA, ribo- ... hloroplast ... the photo- ... any other ... tenance of the chloroplast are not present within it. Chloroplasts, therefore, live as symbionts in the cells of green plants contributing photosynthesis to the overall welfare, but receiving from the host all the needed building blocks for their development.

Replication of chloroplasts by fission were reported in Tobacco by Boasson and Laetsch in 1970 and 1972 and in *Phaseolus* and *Vicia* guard cells and mesophyll cells by Pallas and Mollenhauer (1972). The divid-

ing chloroplasts have well-developed grana and chloroplasts. The constriction may divide chloroplasts equally or unequally. Usually young chloroplasts divide but mature and fully developed chloroplasts have also been made to divide. *Such a replication is independent of the size and specific internal morphology of the organelle.*

The number of chlorophyll molecules required to reduce one molecule of CO_2 or yield one molecule of O_2 constitutes **photosynthetic unit.** This number is usually 200—300 chlorophyll molecules. Special bodies called **quantosomes** have been discovered on the inner surface of lamellar membranes. These are about 160A° by 180A° and about *100A° thick. They can also appear in random array. One quantosome* contains about the same number of chlorophyll molecules as contained in a photosynthetic unit.

The chloropla[illegible]
bodies called the [illegible]
In the Diatoms, [illegible]
cell division but, [illegible]
and reappear in [illegible]

Nucleus (Fig 2.5). It is the most prominent structure of the cell [illegible] cell. [illegible] val or [illegible] iburg as "like a lump of ice in water." The nucleus contans the chromosomes and the genes which, somehow or the other, guide and determine the *character, activities and destiny of each individual cell. A cell may* contain one to many nuclei. In the higher plants the cell generally contains one nucleus but in the lower plants *e.g*, algae and fungi, the cells may contain more nuclei than one. Such multinucleate cells are called the **coenocytes.** In the blue-green algae and the bacteria, there is no nucleus. The nuclear matter is scattered in the centre of the cell. The size of the nucleus varies from 1—500 microns (μ). Generally they measure 5—25 microns. The nuclei always arise from pre-existing nuclei. They never arise *de novo*. A cell without a nucleus cannot live for long and is ultimately dead.

Structure of the nucleus. The nucleus is bounded on the outside by a limiting membrane, called the **nuclear membrane,** which, so far as is known, is quite similar to the cell membrane, and is made up of two distinct layers, each layer is about 75A° thick. The nuclear membrane is composed of proteins and lipids. The two membranes are separated from each other by a space *called* **perinuclear cisterna,** *which varies* in width from about 400—700 A°. The outer membrane may be continuous at various points with the endoplasmic reticulum. There is some evidence that the endoplasmic reticulum forms vesicles around the chromosomes during telophase of cell division. It appears that these vesicles coalesce to form the nuclear envelope. Electron microscopy has also revealed the presence of minute pores in the nuclear membrane of some plants. Presence of granular outgrowths in the nuclear membrane *has also been reported in the pollen mother cell nuclei of*

some angiosperms. The pores are usually found at places where the outer and inner membranes coalesce. It is not clear whether these pores permit free diffusion. Electron micrographs at high magnification indicate that a septum extends across the pore. Long strands have been seen to extend from the nuclear envelope to the mitochondria, golgi vesicles and other cytoplasmic organelles. In some animal cells a thick fibrous layer (300Å thick) is seen next to the inner nuclear membrane. It is termed as **fibrous lamina**. The nucleus is filled with a dense but clear mass of protoplasm, called **nuclear sap** or **nucleoplasm**. It is also known as **karyolymph** The mass of the nucleus stained with nuclear dyes is seen to consist of a fine network of threads beaded with coarser granules. The network is called the **chromatin network** or **nuclear reticulum** The chromatin network during division becomes more clear and becomes visible as a definite number of individual chromosomes. The number of these chromosomes is fixed for a particular species and thus is known as the law of constant chromosomes. For example pea plant has 14 chromosomes in every nucleus of its somatic cells. These 14 chromosomes can be divided into two groups of seven each, one group being derived from male parent and the other from female parent. The full double complement of chromosomes (14 in above case) is referred to as **diploid** ($2n$) number, and basic number obtained from each parent (7 in above case) is the **haploid** (n) number. These chromatin threads are made up of a strongly stainable chemical substance called the **chromatin** or the **nuclein**. The nature of this substance is the nucleo-protein which is a phosphorus-containing protein. This chromatin network can be stained with basic dyes such as *carmine*, *crystal violet*, *haematoxylin* etc. The coarser granules that are studded on the chromatin network are

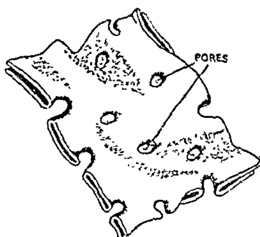


Fig 2.18. It illustrates two-layered structure of the nuclear membrane. Note the pores.

chromatin that

ses a definite

much denser,

than the nucleoplasm. These are known as the **nucleoli**. Weinstraub *et el* (1968) reported the presence of crystals in the nuclei of all cells in the leaves of two species of *Dianthus* (*D. barbatus* and *D. chinensis*).

Chromatin is the hereditary material of the nucleus and the science

e chromosomes are

Chemical analysis

molecular basis of

as revealed that the

: (1) a low molecu-

lar weight protein called **histone**, (2) a more **complex protein (non-histone)** that can be distinguished from histone, (3) **deoxyribose nucleic acid** (DNA) and (4) **ribose nucleic acid** (RNA) (Fig. 2.19). Of these four constituents of this chromatin, DNA (Fig. 2.20) plays a major role in heredity. It is the substance of inheritance that carries the genetic instinct from one generation to the other.

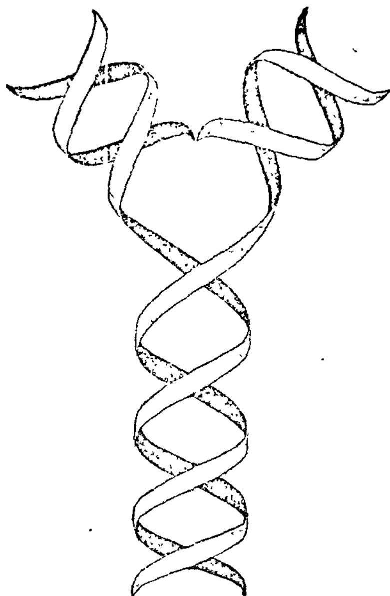


Plate 5. Replicating DNA Molecule.

The chromatin network that forms the substance of the chromosomes can be distinguished into two main types : (*i*) the **heterochro-** and (*ii*) **euchromatin.** The heterochromatin refers to the deep-

the chromosomes and euchromatin he chromosomes in the interphase inction disappears during nuclear division when whole of the chromosome becomes condensed. The two types of chromatin form a continuous fibre. The hetrochromatin is associated with tight folding and coiling of the fibre. The heterochromatic part of the fibre is thick and has a diameter of about 200—300A° whereas the euchromatic part has a diameter of about 35—60 A°. The diameter of DNA molecule is ... to be relatively inert metabolicall ... more active part of the chror ... been shown to be the primary site for incorporatining the RNA precursor.

The Genetic Material

Watson, Crick and Wilkins (1953) elucidated the structure of a DNA molecule. They performed X-ray analysis of the molecules and came to the conclusion that each DNA molecule which is composed of smaller molecules is in the form of two strands that are twisted about each other in the form of a double coil (Fig. 2.20) or a double helix. DNA molecules with one strand (single-stranded) and with more than two strands are also known. The chief molecules that enter into the composition of a larger molecule of DNA are : (1) ... phosphate, (2) ...

... and (*ii*) the *thymine*. All pyrimidines have a basic skeleton of four carbon and two nitrogen atoms in a ring. The purines are represented by (i) ...

... can best be compared to the railings of a ladder that are united to each other by the steps or the rungs. The railings are made up entirely of the phosphate molecules ... igar. The steps or ... Each step or the rur ... the pyrimidine. Th ...

The arrangement of these base pairs is very important and determines the hereditary qualities of the DNA molecule. The chemical composition of the DNA molecule and its total amount is constant in similar types of cells and this constancy is maintained from generation to generation. The quality and the quantity of DNA remains unaltered in the cells derived from the same parent cells.

The question now arises as to how the quality and quantity of DNA remain unaltered in the newly formed cells by division of the parent cells. The DNA in chromatin network (which resolves into

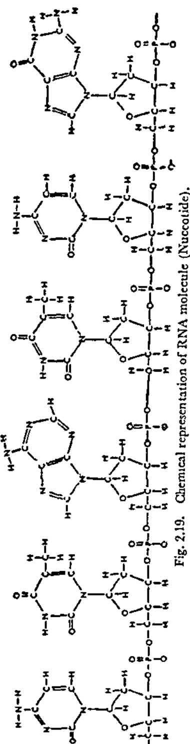


Fig. 2.19. Chemical representation of RNA molecule (Nuccotide).

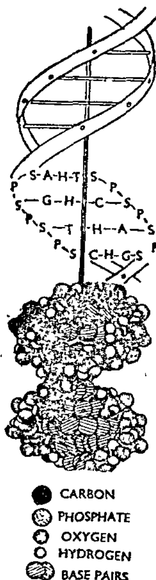


Fig. 2.20. A DNA molecule after Watson and Crick (1953).

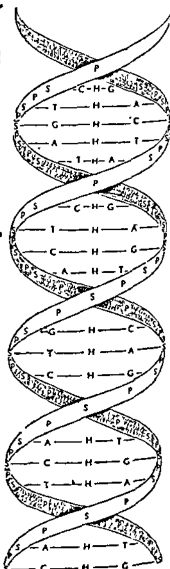
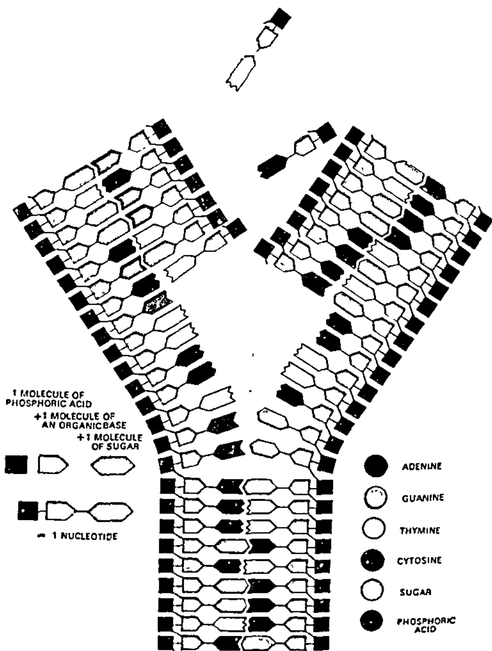


Fig. 2.21. A. DNA molecule. The two helically coiled strands are slightly displaced so as to make the structure clear.



Replicating DNA

weak point which is the hydrogen bond between the two base pairs (a purine and a pyrimidine). This unzipping of the DNA molecule at the weak forces (H-bonds) leaves the two strands apart, each strand with a purine or a pyrmidine base attached to the sugar molecule. Each strand has now the capacity to replicate an exactly identical strand like the partner from which it has separated. Such a replication has been studied in great deal by a number of workers (M. Meselson and F W. Stahl, 1958). It is beyond the scope of this book to go into all the details.

The RNA differs chemically from the DNA in that it contains a ...ose sugar. The ribose sugar has an ...ich is lacking in Deoxyribose sugar. The ... except that the chemical constitution of one of the pyrimidine pair is slightly different and is called *Uracil* instead of thymine. RNA is believed to be formed first in the nucleus and there is sufficient evidence that it is required for the synthesis ... activity are the ... It is, therefore, ... odies is actually the messenger RNA which carries the information from DNA to these sites of protein synthesis. As has already been pointed out the ribosomes which contain mostly the messenger RNA are the principal sites that determine the arrangement of the amino-acids in the protein synthesis. This particular arrangement of the amino-acid is controlled by the structural characteristic of RNA which in turn are determined by the nuclear DNA. So there is a chain of flow of information from DNA to RNA and finally to protein. This protein whose specificity is controlled by DNA through messenger RNA, later on enters into most of the cellular structures. Since these proteins include among their kind all the enzymes that catalyze the innumerable chemical reactions going on in the living cell they must, because of the special function they perform, be regarded as the most important and crucial pieces of machinery of the cellular factory that determines ultimately the product it makes or the service it renders.

Nucleolus (Fig. 2 5). The nucleolus is made up of RNA and proteins and is formed by a particular chromosome at a region known as **nucleolur organiser.** This region may be one of synthesis or collection. It has been ascertained that this region contains **cistrons** for ribosomal RNA. If this organiser region is a length of DNA coding for ribosomal RNA, and the cistrons are actually synthesizing corresponding RNAs, then nucleolar proteins may collect around the active site although originating in some other part of the chromosome. During the interphase stage the nucleolus remains attached with nucleolar organiser and is in close contact with DNA and histone of the organiser.

The ... wo distinct regions : (i) the **pars** ... The former is a structurless c... appears to be a dense mass of filaments, about 50A° thick. The **nucleolonema** is a fibrillar component which often appears as a coarse thread. In plants it appears as a central core with dense granules forming a peripheral localisation. Some granules like the ribosomes are embedded throughout the matrix of the nucleolus and contain both RNA and protein and are usually ... There is no limiting memb- ... have been reported as ... is surrounded by small ... are made up of associated ... The chromatin of these satellites penetrates the nucleolus as irregular strips or regular lamellae. It has been ascertained that as the nucleolus disappears during division the nucleolonema fragments and dispersers into the cytoplasm. It has the power of self-reproduction. Pipkin (1965) studied the nucleoli in the pollen mother cells of *Hippeastrum belladonna* and reported that the nucleoli have vacuoles that contain unique RNA and associated basic proteins with *ariginine-lysine* ratios differing from the basic proteins of the nucleolus proper. They have no limiting membrane. These nucleolar vacuoles contain a heterogenous matrix which is partially fibrillar and is different from the nucleolar matrix. It is, therefore, evident that the nucleolus also performs the main function of protein synthesis. Its disappearance during nuclear division (mitosis and meiosis) also suggests its role as a means of passing genetic information and materials from the nucleus to the cytoplasm.

B. ERGASTIC SUBSTANCES

In addition to the various kinds of living or protoplasmic structures found in the cytoplasm, there are also present a great variety of non-living substances in the cell. These are known as non-living inclusions of the cell. These substances are found in the cytoplasm as well as in the vacuoles. They may also occur in the cell wall. Some of them are ... **ergastic substances.** Some ... present as impurities, ... these substances can be grouped under three convenient headings :—(*a*) the reserve food materials, (*b*) secretory products, and (*c*) the waste products.

Vacuole. The vacuole is non-living and appears to be a 'reservoir' in the cytoplasm, bounded by a differentially permeable membrane. It contains a watery solution of salts, organic substances and waste products of cell metabolism. A young cell possesses numerous small vacuoles, which fuse together forming larger vacuoles, as the cell grows, and in a fully mature cell there may be a single big vacuole in the centre (Fig. 2.6). This big vacuole may occupy 90% or even more of the total volume of the cell. The membrane surrounding the vacuole is called the **tonoplast.** It is composed of proteins and fatty material and has a property of a differentially permeable membrane. Besides a variety of dissolved material, the vacuolar sap contains also some solid

bodies. The contents of the vacuole may be listed as below—(1) **organic acids** such as **malic acid, oxalic acid,** etc. (2) **soluble carbohydrates** *e.g., grape sugar, cane-sugar* and *inulin* ; (3) in some storage cells and in the growing regions the vacuoles may contain *soluble proteins, amino-acids* and *amines* ; (4) some enzymes have also been reported from the cell-sap ; (5) *tanins, latex, glucosides,* and *alkaloids* ; (6) some secretory products like the *anthocyanins* are usually present in the vacuoles of the petals of flowers ; (7) *inorganic salts e.g.,* sulphates, nitrates, phosphates and chlorides. Cotyledon mesophyll cells in maturing seeds of *Gossypium hirsutum* manufacture (Engleman, 1963) aleurone grains by accumulation of proteins and other materials in vacuoles. In early stages of development the vacuoles have been seen to communicate with the endoplasmic reticulum (Engleman, 1965).

(*a*) **Reserve Food Materials.** The protoplasm manufactures its food from the simple inorganic substances like CO_2 and H_2O. The foods thus manufactured are partly used up to make new protoplasm and partly it is broken down to provide necessary energy, and the remaining food is stored as reserve food material in protoplasm of cells, specially meant for this purpose. These reserve materials are used by the protoplasm as and when required. The reserve food may be stored in the form of solid and insoluble particles in the cytoplasm, or it may be stored in solution in the vacuoles. These reserve foods are of three principal types : (1) Carbohydrates, (2) Nitrogenous materials, and (3) Fats.

1. Carbohydrates. These are compounds of carbon, hydrogen, and oxygen derived more or less directly from carbon dioxide and water during the process of photosynthesis. Sugars, starches, celluloses, dextrin and glycogen and inulin are examples of some carbohydrates that are found in the plants. Carbohydrates are the cheapest food and are the chief sources of energy, and also supply carbon skeletons that are necessary for the manufacture of basic components of protoplasm. Most of the carbohydrates are employed in the various industries (paper industry, fibres of various types), and some are employed in the production of alcohol. They have a general chemical formula $C_n(H_2O)_n$. On heating, the carbohydrates form a black mass, which is carbon left behind as a result of escape of water.

Sugars. They are soluble in water and are found in the cell sap. In solid form the sugars are white, crystalline substances that are always sweet in taste. The grape sugar or the glucose (found chiefly in the grapes) is simplest of all carbohydrates and is the first carbohydrate produced as a result of photosynthesis It is converted into other forms of carbohydrates. Other types of sugars are cane-sugar or sucrose (found in sugar cane), fructose (found in many fruits) and maltose found mostly in the germinating seeds.. Structurally the sugars are hydroxylated aldehydes and ketones and may be classed as **monosaccharides,** if the compounds are single units that are incapable of being hydrolysed further, **disaccharides, trisaccharides,** and **polysaccharides,** if more than one unit is present in the molecule. Glucose and fructose are examples of monosaccharide sugars. Cane-sugar

is a disaccharide sugar called sucrose. Maltose is also a disaccharide sugar.

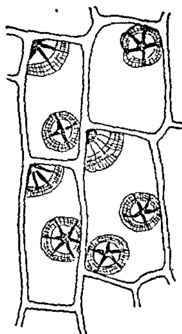
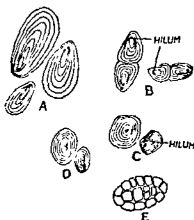


Fig. 2.22. Innulin Crystals in the cells of Dahlia tuber.



[illegible] grains. [illegible] B, [illegible] ains [illegible] E, Compound grain in rice.

Inulin (Fig. 2.22) It is a polysaccharide carbohydrate that is soluble in water and insoluble in alcohol. *It is found in the tubers of Dahlla* and *Helianthus tuberosus.* It is found in solution in the cell sap of these storage organs and can be precipitated in the form of spherical or star-shaped crystals, *if thin pieces of Dahlia* tuber are dipped in alcohol for 6 to 7 days. Thin sections of these pieces can be cut and examined under the microscope. The inuli[illegible] [illegible]tals can be seen across the cell walls. Incomple[illegible] c[illegible] be seen as fan-shaped structures. Inulin [illegible] chemical formula $(C_6H_{10}O_5)_n$. It is m[illegible]hyd[illegible] molecules linked together.

In wheat the grains are round, oval in potato, polygonal in maize, spherical in pea and bean, dumbell-shaped or rod-shaped in the latex cells of some Euphorbias. The size of the starch grains varies between 5—100μ in length. The starch grains of *Canna* are the largest and those of rice smallest. The starch is formed from the glucose and this reaction is accelerated by the enzyme phosphorylase. The starch is synthesized by the leucoplasts in the storage organs that are non-green and such a starch is known as **storage starch.** It is consumed in huge quantities by man and animals. The starch synthesized by the chloroplasts in the green cells of the plant is called the **assimilation starch.** Starches are generally made up of two components ; the more soluble component called the **amylose** and the insoluble **amylopectin.** Both these components are the derivations of glucose and show a differential staining with iodine. The amylose turns deep blue whereas the amylopectin turns light blue.

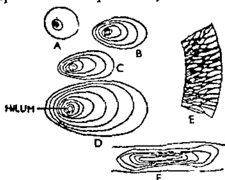


Fig. 2.24. (A—F) A—D. Starch formation in the chloroplasts of *Pellionia daveauana* E. Submicroscopic structure of one layer. F. dumbell-shaped starch grain from the milky latex of *Euphorbia splendens* (E. after Frey-Wyssyling, A-D. after *Strasburger*).

Structure of the starch grain as viewed under the light microscope reveals every grain to consist of a definite rounded or elongated structure, called the **hilum.** Starch is deposited around this structure (hilum) in the form of layers (Fig. 2.24). The layering may be readily visible in some grains or invisible in others. Majority of the starch grains show this layering and are called stratified starch grains. If the layers are laid down all on one side of the hilum, the grain is said to be **eccentric**(*e.g.* Potato), and if the layers are laid down concentrically around the hilum the grain is called **concentric.** Recent investigations have shown that the deposition of these layers is not dependent upon external influence *e g.*, light and temperature, but are dependent upon certain endogenous rhythms. In potato two to three layers are formed in one day. In concentric grains the hilum is in the centre (*e.g.*, wheat, rice, maize, bean, pea, etc.). Concentric types of starch grains are very common. Starch grains may be classified as simple if they occur singly with a single hilum. If more than one grains occur together with their separate hila, they form a group and are known as compound grains. Compound grains are commonly found in rice and oat. Starch has the same chemical formula as inulin, but is insoluble in both water and alcohol. It is turned blue or black in an aqueous solution of iodine. In water at 60°—80°C they break down to form a paste. If we heat starch in the absence of water, it changes into a water soluble substance called *dextrin.* At room temperature the starch grains swell, if immersed in a solution of sodium or potassium hydroxide Starches are converted into sugars if treated with concentrated sulphuric acid.

Dextrin :—It is not found as a food reserve in the plants but is one of the produces formed during the synthesis of starch from glucose.

Glycogen :—It is a characteristic reserve food material of some algal groups (Cyanophyceae) and all the fungi. It turns brown when treated with iodine. Glycogen is absent in the higher plants. It has the same chemical formula as that of starch $(C_6H_{10}O_5)_n$. It is soluble in hot water and occurs in the form of granules in the cytoplasm.

2. **Nitrogenous materials** :—Proteins, amino-acids and amines are the principal reserve food materials that belong to this group. They are very important and indispensable foods that enter into the composition of protoplasm.

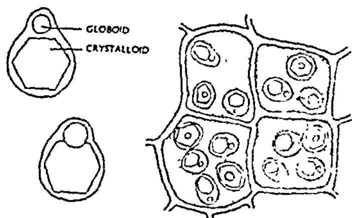


Fig. 2.25. Protein grains from the endosperm of castor oil seed

Proteins (Fig. 2.25). They are probably the most important and vital chemical constituents of living organisms. They have been chemically defined as high molecular weight polymers in which the building blocks are the amino acids. They are made up of carbon 50—51%, hydrogen (7%), oxygen (20—25%) and nitrogen (16—18%). If proteins are hydrolyzed (*i.e.*, broken down in the presence of water), they break down into simple nitrogen containing molecules called the amino-acids. The proteins may or may not be soluble in water but they are soluble in strong acids and alkalis. Modern physical methods have shown us quite clearly that in the formation of a protein molecule, the amino-acids are joined together through bonds between carboxyl group of the amino-acid and the amino (NH_2) group of another by removal of water.

The proteins can be classified into two main types—**fibrous proteins** and **globular proteins**. The fibrous proteins are insoluble in water and other aqueous solutions and form many structural parts of cells. The globular proteins are soluble in water or in aqueous solutions. They are of two main types—**simple proteins** and **conjugated proteins**. The simple proteins are of six types:—**protamines** with low molecular weight and [illegible]; **histones** (with high molecular weight and [illegible]); **albumins** soluble in water and dilute neutral salt solutions; **globulins**

(insoluble in water but soluble in neutral salt solutions) ; **glutelins** (soluble only in dilute acid or alkali) ; **prolamines** (soluble only in 80% alcohol).

In conjugated proteins the protein molecule is always attached to a **non-protein group** or a **prosthetic group.** In **lipoproteins** this prosthetic group is a lipid (found in mitochondria, golgi bodies, cell membranes etc.) in **nucleoproteins** a nucleic acid is present and the protein part is always a **histone** ; in **glycoproteins** a carbohydrate is attached ; in **chromoproteins** pigments like chlorophyll and haemin are attached to the protein group .

Functionally proteins can be classified as **food storage proteins, structural proteins** and **enzymes.**

The proteins are stored in various kinds of storage organs in plants. They are found in plenty in the seeds *e.g.*, sunflower (30%), rice (7%), wheat (12%). Seeds of pulses usually contain 25% protein. Aleurone proteins (Fig. 2.25) or aleurone grains are a type of storage protein found abundantly in the endosperm of seeds *e.g.*, castor oil, maize grain, etc. The aleurone protein usually encloses, in its oval or spherical body, a **crystalloid** which is larger in size than the second rounded or globose structure called the **globoid.** The crystalloid is proteinaceous in nature whereas the globoid is a mineral body and is a double phosphate of calcium and magnesium.

Amino-acids. They are simple nitrogenous food materials that enter into the composition of proteins. These are extremely important plant products. They are amino-substituted fatty acids. Thus they contain a—NH (amino group) and a—COOH group (carboxylic group), or more than one of each. Those amino-acids with one amino and one carboxylic group are called **neutral.** Those with two amino groups are called **basic** whereas those with two carboxylic groups are called **acidic.** Some plant products have $>$NH rather than $—NH_2$ group. There are known as **imino-acids** *e.g., proline.*

They usually occur in solution in the cell sap. During translocation of food the proteins generally break down into amino-acids. There are hundred amino acids known in nature. Out of these only twenty enter into the composition of proteins.

The important amino-acids are : *Valine, Lysine, Theonine, Leucine, Tryptophane, Methionine, Isolevicine, Phenylalinine,* etc. The various types of proteins in whose composition these amino-acids enter are, *Insulin, Haemoglobin, Albumin, Keratin, Fibroin.*

Fats and Oils. They are compounds of carbon, hydrogen, and oxygen. The last two do not occur in the same proportion as in the carbohydrates. Only a little percentage of oxygen enters into the composition of fats and oils. Nitrogen is altogether absent. They are concentrated sources of food and provide more calories [illegible]
proteins and carbohydrates. They
ethnol are used to extract them

found in smaller or greater amounts in all plants and usually occur as minute globules in the protoplasm and are unable to be transported as such from cell to cell. They are abundant in fatty seeds and fruits *e g*, *Arachis hypogea*, *Linum*, etc. Fats are solid at ordinary temperatures whereas oils are liquids. Fats are synthesized from glycerine and fatty acids in the presence of an enzyme called *lipase*. The fatty acids (butyric acid, octanoic acid, palmitic acid, stearic acid) and the glycerine are formed in the protoplasm from the carbohydrates during the process of respiration.

The fats and oils have a great economic value and are important sources of food, soaps, lubricants, paints etc. The groundnut-oil on hydrogenation yields a fat called *Ghee*. The coconut oil, almond oil, olive oil, linseed oil, mustard oil, etc. are of great economic value.

(*b*) **Secretory Products.** These are secreted by the protoplasm and are not useful as nutritional products but may help or accelerate the various reactions in the cell. Chlorophyll is a green colouring matter secreted by the chloroplasts and is a vital product that helps in the remarakable process of photosynthesis Anthocyanins are also secretory products of the protoplasm and are stored in the cell-sap in vacuoles. They impart colour to the petals of various flowers and enhance their beauty thereby helping to attract insects. Nectar is another useful secretion of protoplasm of special secretion glands called the nectaries that are present in flowers. Insects visit the flowers mainly for obtaining nectar. Honeybees convert this nectar into honey which is extensively used by man as a food.

(*c*) **Waste Products.** They are excretions of the plant and in the absence of any excretory system in the plant these substances are stored in the dead cells *e.g.*, bark cells, dead cell ... and
lysigenous cavities, etc. These products
bolic activities of protoplasm and are alsc
of plants. In their nature they may be regarded as **Nitrogenous** and **Non-Nitrogenous.**

1. **Nitrogenous Waste Products** *Alkaloids* are the nitrogenous wastes of plants and have found their use in the medicine industry. They are complex amines whose function in the plant is not known. Many of them produce interesting physiological reactions in man and
cure m ... for
curing ... in
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as drug, morphine in poppy is also a common drug. Other alkaloids are: nicotine in tobacco, caffine in coffee and tea, strychnine in *Nuxvomica*, etc.

2. **Non-nitrogenous Waste Products.** Gums, resins, latex, organic acids, tannins and kinds of mineral crystals are the chief non-nitrogenous waste products.

Gums. They are soluble in water and swell up in it to form a viscous mass. Gum exudes from the twigs and stems of many plants. Gum arabica is the most common type of gum obtained from the twigs

and stems of *Acacia arabica*, *Acacia modesta*, and *Acacia senegal*. It exude in the form of a thick juice from the bark of these trees. Gum tragacant is produced from several species of *Astragalus*.

Resins. They are the chief products of most of the coniferous trees. They are secreted by a layer of secretory cells surrounding the resin ducts found in the leaves and stems of various species of *Pinus*. It is ... source of turpen-

Resins are insoluble in water but soluble in alcohol and turpentine. Canada balsam is also a resinous product of *Abies balsamea*.

Organic acids. They are produced by various chemical processess going on in living cells and exist in vegetable juices and are often combined with peculiar bases and alkaloids. There are several types of acids found in plants *e.g.*, citric acid in the fruits of orange, lemon, lime; tartaric acid in the juice of grapes and in combination with potash in tamarinds; malic acid in the fruits of apple, gooseberry; tannic acid in oak bark and nut galls; gallic acid in the seeds of Mango; meconic acid in the juice of *Papaver somniferum*; oxalic acid in species of *Rumex*, *Oxalis* and in the pitcher of *Nepenthes distillatoria*.

Latex. It is an emulsion of various ...

unicellular as in *Ceropegia* (Fig. 2.26), or may be branched and compound as in *Taraxacum* (Fig. 2.26) and many species of *Euphorbia*. These ducts are formed lysigenously. Latex may be coloured milky or may be colourless. It contains a variety of nutritive substances such as starch, sugars, proteins, etc. Waste products such as alkaloids, tannins, resins, gums etc., are also formed in it. The latex of

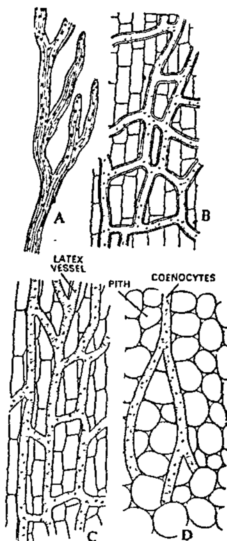


Fig. 2.26. Latex ducts and vessel. A, a branched unicellular latex duct from *Ceropegia*.
B, a compound latex duct from the root of *Taraxacum*.
C, a latex vessel from *Argemone mexicana*.
D, latex cells from *Euphorbia*

some plants is very useful as the latex of the rubber plant is used in the most flourishing rubber industry. In poppy the latex may be coloured. Latex is milky in many species of *Euphorbia* and *Calotropis.*

Volatile or essential oils. They occur in the stems, leaves, flowers and fruits of many odoriferous plants and can be procured by distillation along with water. They are called essences or scents and contain the concentrated odour of the plants. They usually exist ready-made. Some of them consist of only carbon and hydrogen *e.g.*, oil of turpentine procured from *Pinus* and *Abies* ; oil of juniper, procured from *Juniperus* ; oil of lemons and oranges and oil of citrus, from the rind of fruits of these plants ; and oil of neroli from orange flowers. A second series contains oxygen in addition to carbon and hydrogen *e.g.*, oil of cinnamon, from *Cinnamomum zeylanicum* ; otto or attar of roses, from various species of *Rose* ; oil of peppermint from *Mentha viridis* , oil of caraway, from *Carum carui* ; oil of cloves, from *Caryophyllus aromaticus*. Oils of this kind are also procured from many plants of the family *Labiatae* A third series of oils have also sulphur in their composition *e.g.*, oil of garlic, oil of onion, oil of *Assafoetida* and oil of mustard.

Tannins. They are common constituents of all the plants and are present in smaller or greater amounts in the cell sap. Their presence in the cell walls of dead tissues and in the heart wood makes these [illegible] immune to the attack of insects and [illegible] ie tannins have a bitter taste and their [illegible] their decoction bitter. The tannins [illegible] *Ac*[illegible] kahta, which is applied to the bete[illegible] betel nuts (which also contain tanni[illegible] mixed with some iron salts the tann[illegible] hides is very well known. They also form important constituents of some medicines. They are compounds with complicated chemical structure and do not contain nitrogen.

Mineral Crystals They are usually found in the cell cavity and in the cell wall. They probably owe their origin to the reaction between the acids produced by the plants *e.g.*, oxalic acid, carbonic acid etc., and the alkaline matters, as lime and potash. The crystals usually lie loose in the cells, but some are also suspended into the cell cavity from the cell wall. Sometimes, only a single large crystal fills up the entire cell cavity, sometimes, they radiate from a common point and, sometimes, they occur in the form of bundles and lie parallel. They vary in shape and size. The usual mineral crystals found in the plants are crystals of calcium oxalate, calcium carbonate and silica.

Silica. It is a common constituent of the cell walls of the various plants. Silica crystals may be embedded in the cell wall or form an encrustation on it. The leaves of grasses, wheat, maize, sugar-cane and stem of *Equisetum* have rich deposition of silica on their walls. Its presence makes the leaves and stems rough.

Calcium Carbonate Crystals. These crystals have been reported [illegible]om within the cells of Banyan leaf (*Ficus benghalensis*) and some

members of the families *Acanthaceae*, *Cucurbitaceae*, *Urticaceae* etc. In the leaf of Banyan they have been seen to occur in grape-like clusters hanging from a stalk that is attached to the cell wall. The name *Cystolith* (Fig. 2.27) is given to such a cluster. During its formation in the epidermal cell of Banyan leaf a stalk-like protuberance of the inner cellulose wall is given out and the crystals of calcium carbonate start depositing on this stalk. In *Momordica* double cystoliths (Fig. 2.27), and sometimes, a group of cystoliths is found in the epidermal cells.

Crystals of Calcium Oxalate. They are widely distributed metabolic end-products and are very common in plant cells and usually occur in vacuoles of cells. They are of different shapes and sizes. They may either contain monohydrate [$Ca(C_2O_4)$. H_2O] or the dihydrates [$Ca(C_2O_4).2H_2O$] depending upon the conditions under which they develop. If we cut a section of the leaf of *Colocasia* (kachalu) we will find that some cells contain star-shaped aggregation of crystals (Fig. 2 27). These are known as *Sphaeraphides* or *sphaero-crystals* or *Conglomerate crystals*, and are also met with in the cells of the stems of

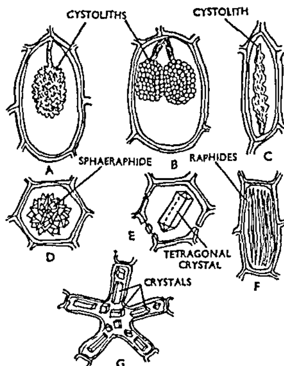


Fig. 2 27. (A—G). Mineral crystals.

[illegible]

G, Various shapes of crystals of calcium oxalate from the petiole of *Canna* leaf.

Opuntia, *Zizyphus*, in the mid-rib cells of *Cycas revoluta*, in the cells in the petioles of Arum lily, *Riccinus communis* (Castor, Arind), and in the mesophyll cells of *Nerium odorum* (kaner), *Thevetia nerifolia* and *Eucalyptus*. In a section through the petiole of the leaves of *Pothos aureus* and *Bougainvillea*, we will come across bundles of needle-like or acicular crystals. Such crystals are known as *raphides* (Fig. 2.27). The needles may even occur singly in the cells. Octahedral crystals have commonly been seen in the cells of the leaves of *Begonia rex*. Crystals of rectangular shape are found in the outer covering of the seeds of *Ulmus campestris*. Rod-shaped and minute crystals of many shapes are present in the cells of the petioles of *Canna* leaves. Cubical prismatic, triangular, and other shapes of crystals are also present in the cells of various organs of plants. Sepals of *Dianthus* and *Prunella* contain solitary cubical crystals

3

THE CELL-WALL

INTRODUCTION

It is a characteristic feature of the plant cell and is non-living ... The cell wall is absent in ... plants. Even in the higher ... male gametes and ... They are naked ... tilisation when the ... arance of wall at ... to develop into the embryo which is going to be the future plant—a plant that has to lead an independent existence and has to adapt itself to the environmental strains and stresses. The cell wall gives rigidity and support to the tissue ... It is the skeletal frame-work of the ... The cell wall is also intrinsically ... ion and water relations of a plant. Since it surrounds all cells, all fluxes of water and solutes into and out of a plant cell must cross the cell wall, usually by diffusion. Cell walls vary from tenths to tens of microns in thickness and generally are divided into three regions. The primary cell wall surrounds meristematic cells as well as the elongating cells. The cell wall often becomes thickened by the elaboration of a secondary cell wall inside the primary one which makes the cell much less flexible. The cell wall ... region between the adjacent cells. ... t is mair ... ich caus ... together. Cellulose is also present in ...

... composed of jelly-like pectic substances and is called the middle lemella.

The formation of the cell plate begins in the metaphase stage. It seems that proteolytic enzymes first decompose the protein structure of the cytoplasm and spindle fibres. Lipid granules then accumulate on the

equatorial plate and are hydrolised by lipase. Estrease is the first enzyme identified in the cell plate followed by lipase; acid phosphatase has also been found in the cell plate. During the anaphase and telophase stages the golgi complex appears to produce a large number of vesicles.

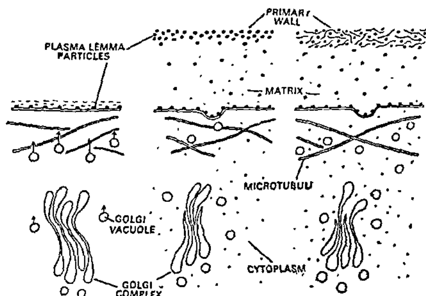


Fig. 3.1. It illustrates the scheme of subsequent steps in cell-wall formation of the green alga *Chlorella*. A, cortical region of the cell with the plasmalemma covered with particles and a sub-adjacent Golgi complex. B, accumulation of matrix material carried to the surface by Golgi vesicles. The plasmalemma particles become detached and move to the outer periphery of the matrix. C. Primary wall formation in the region where the particles are concentrated. *(After Muhlethaler, 1967)*

At first these vesicles are small and appear between the spindle fibres. The vesicles condense and merge, grow larger and move to the equator of the cell where some fuse to add to the developing cell plate. Golgi-vesicles then fuse to form new cell membranes. The formation of the cell plate is also characteristic for the formation of the walls of pollen tubes, root hair, root tip cells and green algae. The endoplasmic reticulum associates closely with the formation of the cell plate (Fig. 3.1). The endoplasmic reticulum bridges the newly formed wall and becomes a component of the plasmodesmata. The outer surface of the newly formed cell-membrane adjacent to the newly formed cell wall has been found to be covered by particles of about 150·A° in diameter. They do not appear on the inner membrane surface. These particles are in some way involved in the synthesis of cellulose fibrils. The golgi complex produces the substances of the noncellulose matrix which are released to the cell surface of the protoplast. The particles on the outer membrane become detached and move to the outer surface of *the non-cellulose matrix. At this time, the first cellulose fibrils become* apparent (Fig. 3.1, C).

More **elementary fibrils** are continuously made and these 'ls maintain the synthesis of cellulose. These fibrils can aggregate

4

into coarse bundles of **cellulose fibrils.** An **elementry fibril** represents one molecule that is folded into a ribbon which is subsequently wound as a tight helix.

Increase in the size of the young cells (regions of elongation in the root tip and stem tip) is accompanied by a corresponding growth of the cell wall. This growth involves some physical and chemical changes in the cell wall. The important physical changes include the growth of the cell wall in si[illegible] deposition of some [illegible] pectic compounds o[illegible] wall. These chang[illegible] ilage, and some mi[illegible] These physical an[illegible] below in detail.

A. PHYSICAL CHANGES :

1. Growth of the cell wall in size or surface extent This implies the growth of the cell wall in size during the early stages of cell elongation. The newly formed cells in the growing regions tend to elongate and grow in size. This is the result of rapid chemical or metabolic changes that are taking place in the cytoplasm. During this growth of the cell the vacuoles also appear, grow bigger and as a result exert a stretching force on the cell wall. The structural components (cellulose) of the cell wall under the force of stretching leave spaces for the intercalation of new particles of wall material that are secreted by the protopl[illegible] between the[illegible] **ception.** [illegible] Nageli. L[illegible] proposed that new cellulose was introduced only into certain areas of the cell wall which first became thin and were thinly covered by microfibirils The areas which did not become filled up become pit-fields.

Protoplasmic tip growth theory was also advanced to explain cell growth. This idea arose from the fact that some cells have a very thin covering at the end. It was proposed that the cell ends were in fact naked, the protoplasm growing forward and later forming a wall around itself.

2. Growth of the cell wall by apposition. During this process the new wall material is not intercalated between the original wall material, but it is simply laid down on the surface of earlier formed walls. The new wall material is laid down in the form of thin layers or plates that are secreted by the protoplasm. The material [illegible] the [illegible] to [illegible] in [illegible] ial [illegible] wa[illegible] wall material is added to the cell wall and forms the secondary the cell. If the materials composing the secondary wall are of

densities, it gives a laminated appearance to the wall. The idea of apposition was later held in a new theory called the **multinet theory**, proposed in 1950. The theory maintains, as shown electronmicroscopically, that the microfibrils are laid down transversely to the cell axis and that successive layers are laid down from the inside, so that the older layers are being continuously pushed outwards.

The middle lamella is often clearly recognisable between the adjacent cells. It is surrounded on either side by the primary and secondary walls. Sometimes, a tertiary wall which is mainly composed of cellulose, is also secreted next to this secondary wall. The tertiary wall may or may not be clearly differentiated from the secondary wall. Both these walls constitute the secondary thickening of the cell wall. The primary wall and the middle lemella (the original cell plate secreted *during cytokinesis) are also sometimes not clearly distinguish*able and may be together referred to as middle lamella.

PLASMODESMATA In c ... between the adjacent cells, ... jacent walls. If we observe ... scale, we find that the primary walls of the adjacent cells show minute pits at the same point. These pits represent areas that remain unthickened. In living cells these pits permit protoplasmic strands to pass through them. The protoplasm of the cells is connected with each other by the fine protoplasmic stand that pass through these pores. These protoplasmic connections are called the **plasmodesmata** (Fig. 3.2). Singly such a strands is called **plasmodesma**. These strands bind together the protoplasts of the neighbouring cells into a large community called the **symplast** These plasmodesmata also *facilitate the movement* of food material and information from cell to celt. Plasmodesmota can be demonstrated by special staining techniques and are best seen in the epidermal cells, cambial cells and other parenchymatous cells. They are also clearly visible in the endosperm cells of the date seeds.

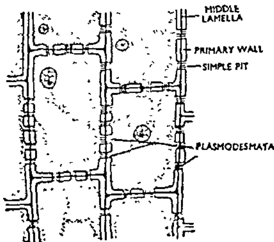


Fig. 3.2. Plasmodesmata in the cells from a thin peel of onion.

Type of thickening of the cell wall. The cells stop increasing in size and enter the phase of maturation. During this phase, the cells modify themselves according to the function they have to perform. During their maturation phase the cells may undergo additional or secondary thickening by the appo-

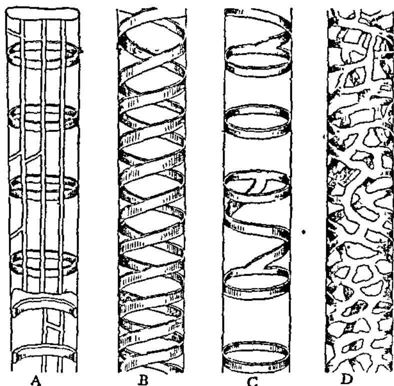


Fig. 3.3. Various types of thickenings of cell wall. A, Annular; B, Spiral, C, Annular and spiral together; D, Reticulate.

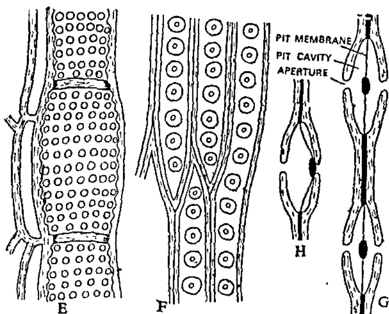


Fig. 3.3. Pitted thickenings; E, Simplepits, F, Bordered pits; G, Bordered pits in L.S showing torus in the centre; H, Torus closing the pit aperture.

sition of new materials *e.g.*, cellulose, lignin, suberin, cutin etc. Some cells *e.g.*, parenchyma cells remain unthickened. The cells in some parts of the plant *e.g.*, pericycle, phloem, xylem, and sometimes in the cortex undergo heavy thickening of their walls. These thickening materials are secreted by the protoplasm and may be laid down in a more or less uniform manner giving the wall a stratified appearance. This laying down of the secondary wall material, when the cell has ses the volume of the protoplast. In some tracheids, etc., the thickening may en- cavity or the lumen. Such cells are dead cells and have no protoplasm. They mainly serve the function of *mechanical support.*

In the cells of tracheids and wood vessels, the thickening material of the secondary wall may not be laid in uniform thickness but may form special patterns. The whole of the wall is not thickened. Only the places where thickening material is laid down in the form of patterns are thick and the rest of the wall remains thin. Such thickenings may be called localised thickenings. Such thickenings may be of the following types :

1. **Spiral thickenings**, (*Fig. 3.3, B*). *In this case, the thickening* material is laid down in the form of a spiral band. The number of spiral bands may be one or more than one. In the seed plants this thickening is present usually in the primary or secondary tracheidal cells of xylem. In *angiosperms, this type of thickening is common in* the vessels or tracheae.

2. **Annular thichenings** Fig. 3.3, A). In this case, the thickening material (lignin) is laid down in the form of rings that are placed one above the other in the interior of the primary wall. The rest of the wall remains unthickened. This type of thickening is also common both in the vessels and tracheids of the xylem.

3. **Reticulate thickenings** (Fig. 3.3, D). Such a thickening results when the thickening material is laid down in the form of bands that form a sort of network leaving irregular meshes of unthickened portions of the wall. The thickening is common in vessels of the angiospermic stems, roots, and leaves, and also in the protoxylem tracheids.

4. **Scalariform or Ladder-like thickenings**. During such a thickening, the thickening matter is laid down in the form of transverse bands which appear like rods or rings of a ladder. The unthickened areas between the successive thickening layers appear like transverse pits. Xylem vessels and tracheids in protoxylem show this *type of thickening.*

5. **Pitted thickenings** (Fig. 3.3 E—G). In this type of thickening, the secondary [illegible] leave certain unthicker[illegible] is uniform throughout exc[illegible] pits are of two kinds : (1) **simple pits** ; and (2) **bordered pits.**

Simple pits (Fig. 3.3, E). The pits are said to be simple when ey have a uniform area throughout their depth and there is no arch-

ing over of the secondary wall. The shape of the simple pits may be circular, oval, polygonal, irregular or even elongated. They are always formed in pairs on either side of the middle lamella which forms a **closing membrane** of the pit. It is also known as the pit membrane. In the simple pits the closing membrane is generally smooth and is not [illegible] ts that occur exactly opposite to each other [illegible] cells form a morphological and a function- [illegible] pit pair The unthickened portion of the secondary wall is called the pit cavity. The **closing membrane** separates the two pit cavities. The opening of the pit towards the cell cavity or lumen is called the **pit aperture** If two simple pits occur opposite to each other, they form a **simple pit pair** (Fig. 3.4, A). Sometimes, there is only one pit, there being no pit on the other side in the adjacent cell. Such a simple pit is called the **blind pit** (Fig. 3.4, B). The simple pit may have a pit cavity with uniform diameter or the pit cavity may become narrow or may widen towards the pit aperture. They occur in collenchymatous cells, sclereids, phloem fibres, and, sometimes, in ordinary parenchymatous cells. They are present in the living as well as dead cells. Their presence is also noticed in the tracheids and vessels of some angiosperms. In the stone cells or the sclereids the pits appear as fine channels or canals on either side of thin middle lamella and serve to connect the lumen (cell cavities) of the adjacent cells. These canals may even be branched and,form a **branched simple pit.**

Bordered pits. The bordered pits (Figs. 3.3, F and 3.4) differ from the simple pits in : (1) the cavity of the pits is not uniform but is broader along the middle lamella and goes on becoming narrower as it proceeds towards its opening or the aperture into lumen ; (2) the [illegible] sort of [illegible] extends [illegible] closing [illegible] s and is distinctly swollen in the centre (opposite the pit apertures) to form a **torus**. The cavity formed by the overarching of the secondary wall is called the **pit-chamber** and its opening into the cell lumen is termed as a **pit aperture.** Sometimes, the overarching secondary wall is very thick (Fig. 3.4, E) and forms a **pit-canal** with one end towards the pit chamber and the other towards the cell lumen. The former is called **outer aperture** and latter **inner aperture.** The bordered pits are present in tracheids of gymnosperms and angiosperms, in the wood vessels of angiosperms. The shape of the bordered pits in surface view is generally rounded or oval. The torus in the bordered pits regulates the flow of materials from cell to cell, because it closes the aperture of the pit when pushed to one side *i.e.*, when it becomes lateral in position (Fig. 3.3, H). The torus is generally bigger in diameter than the aperture of the pit and can, therefore, close it. The torus in *Cedrus* has a fringed margin. This is a characteristic feature of this genus. In some conifers the pit membrane around the torus is perforated. Torus is characteristic of bordered pits of Gnetales and some Coniferales. It is rare in angiosperms.

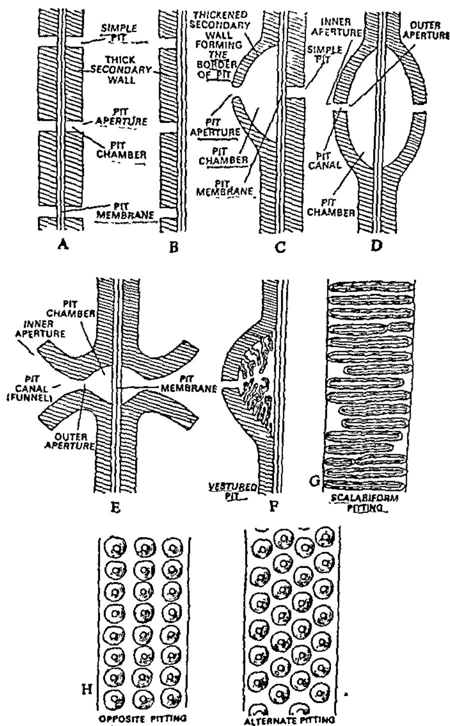


Fig. 3.4. (A—I). Various types of pits, their structure and arrangement A—B, Single pits ; C—E, Bordered pits ; F, Vestured pit ; G, Scalariform pitting ; H, Opposite pitting ; I, Alternate, pitting.

The bordered pits may occur opposite to each other and form a **bordered pit pair** (Fig. 3.4, D). Sometimes, out of the two opposite pits one is a bordered pit and the other is a simple pit. Such a pair is called **half-bordered-pit pair** (Fig. 3.4, C). In many cases there is one large compound pit and opposite to it there are two or more small simple pits. Such a condition is called **unilateral compound pitting**.

In some dicots (some *leguminosae, cruciferae, myrtaceae* and *caprifoliaceae*), the secondary wall of the pit aperture or the pit chamber is produced into simple or branched sculpturings (Fig. 3.4, F). Such bordered pits are called **vestured bordered pits.**

The pit aperture (opening of the bordered pit towards cell lumen) may be circular, oval, elliptical or elongate and linear. With the thickening of the arching secondary wall of the bordered pit the pit-chamber becomes narrow and the **pit canal** (canal formed by thickening secondary wall and having inner and outer apertures) becomes long. The inneraperture (aperture of pit canal towards the cell lumen) in such cases becomes long and narrow. In case the secondary walls become very thick, the inner aperture becomes longer than the pit-chamber, whereas the outer aperture remains circular. The pit canal in such pits becomes funnel-shaped. The long and narrow inner apertures of such pit pairs may be parallel or crossed. When such elongated pits are arranged in a ladder-like manners the arrangement is called **scalariform pitting** (Fig. 3.4, G). In case the pits are circular or oval, their arrangement may be opposite or alternate (Fig. 3.4, H, I).

Chemical Nature of The Cell Wall. The cell wall in plants is made up of a novelty of chemical substances that are secreted by the protoplasm. The chief constituents of the cell wall are: cellulose, pectic compounds, cutin, suberin, mucilage, lignin and some mineral substances, like silica, calcium, oxalate, etc.

Cellulose. It is a common constituent of the plant cell walls and it secreted by the protoplasm. Cellulose is formed from sugars with a general formula $(C_6H_{10}O_5)_n$, where the value of *n* is not known. The entrance of cellulose into composition of plant cell walls is due to the fact that it ensures an efficient support because the cellulose molecule is a macromolecule having a long chain of sugar (glucose) molecules. Each molecule of cellulose is built up of 60 chains of glucose molecules and each glucose chain has 1000 to 3000 anhydrous glucose molecules. These chains are inter-connected with each other by other chains of the same substance and form a sort of **crystal lattice** which eventually reaches visible dimensions. A cotton fibre wall is made up of a billion cellulose chains which are grouped together to form fibrils that run along the entire length of the fibre wall. There are spaces between these cellulose fibrils which give the wall its flexibility. Estimates reveal that a cotton fibre wall is made up of 10 trillion cellulose molecules which are in turn composed of 60 quadrillion glucose molecules. Cellulose is a very useful substance and is used as food by the herbivorous animals and in paper industry, cotton and silk industry. The cellulose wall is elastic, transparent and permeable to water.

Pectic Compo ... cementing materials between the ... are mainly composed ... in pectate and methylated calcium. Pectic compounds generally ... three forms in the plant cell walls. These are : protopectin or insoluble pectose, soluble pectin and pectic acid which is also insoluble. All the ... consist primarily of 1,4 –linked ... boxyl groups of which ... charge. This negative charge leads to the tremendous cation-binding capacity of the cell walls.

The cell wall matrix also contains liquids, noncellulosic polysaccharides, a small amount of protein bound and free water, appreciable calcium, other cations, and sometimes silicates and hemicelluloses. The lignins are complex phenyl-propanoid polymers with varied sub-unit residues and constitute the second most abundant class of organic molecules in living organisms. Lignins tend to be hydrophobic and thus act as water-proofing agents for the cell walls. Lipids and cutin also occur in the cell walls and are quite important components of the cell wall. They also act as water-proofing agents due to their hydrophobic properties.

B. CHEMICAL CHANGES IN THE CELL WALL :

The cell wall undergoes many chemical changes during its growth in thickness. These are :—

1. **Lignification** This chemical change of the cell wall consists in ... along the original cellulose cell wall ... cellulose into lignin. There may be a ... tire wall or there may be a partial ..., the wall is said to be composed of lignocellulose. Lignification of the cell wall usually occurs in those cells that are destined to give support to the plant or have to serve as conducting channels Lignified cells are generally dead and their walls become hard. Such walls are permeable to water. Lignification occurs in phloem fibres, tracheids and wood vessels. Lignin is a chemical substance of a complex nature. It is believed to be made up of a large number of units of aromatic nuclei whose method of linking together is not known. It is stained deep yellow with iodine solution and violet red with phloroglucin.

2. **Cutinization.** This change involves the transformation of cellulose or pectic substances of the primary or secondary wall into *cutin*, which forms a continuous layer, called the *cuticle* It generally forms the skin or outermost covering of the stem, leaves, and some fruits. It is impermeable to water and is only slightly permeable. Due to its waxy nature, it checks evaporation of water from the inner tissues of exposed plant surfaces. Cutin is made up of highly polymerised compounds consisting of fatty acids. The epidermal layers of stem and leaves contain cutin. It stains yellowish brown with chloro-zinc-iodine.

Electron micrography of cuticle has shown it to be an amorphous sheet in majority of cases, but recently sections of cuticle have shown it to be made up of faint layers of lamellae parallel to the cuticular surface.

In the epidermal cells there are two distinct layers (Fig. 3.5) : (*i*) inner layer made up of cellulose and encrusted with **cutin** and usually known as **cuticular layer** ; and (*ii*) an outer layer adcrusted on the cell wall of almost pure cutin and is called the **cuticle.** Both these layers, called the **cuticular membrane**, are apparently separated from the cutin-free inner parts of the wall by a thin layer of pectic substances. The cuticular layer produces **cuticular flanges**, which are thrust down between the epidermal cells below for some distance. The cuticle is not a part of true cell wall, but is a continuous acellular sheet.

Wax is often secreted in the from of grains, plates or rods on the surface of cuticle (Fig. 3.5). It forms characteristic glaucous 'bloom' on the surface of leaves and fruits. How the wax comes to the surface of cuticle is not known. It has been suggested that it comes up through some pores in the cuticle. Such pores have, however, never been seen under the electron microscope.

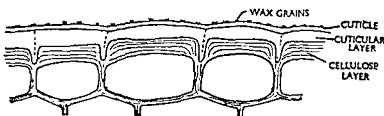


Fig. 3.5. Epidermal cells from the leaf of *Agave*, showing cuticle and a layer of wax grains.

3. **Suberization.** It is effected by the deposition of suberin, which is closely related to cutin in its chemical composition. It generally occurs in the walls of cork cells, which are impermeable to water and also prevent evaporation of water from inner tissues of plants. The cork of commerce has suberised cell-walls and is, therefore, used for bottling. Cutin and suberin are mixed in the casparian strips of the endodermal layer of some roots. It has been obsreved under the electron microscope that suberin layers exist in the form of parallel lamellae, which have wax between them. The suberin layers are bi-refringent.

4. **Mucilagination** It is the chemical conversion of cellulose of the cell wall into a substance known as **mucilage.** Mucilage, readily absorbs water, swells up, and has a capacity to retain water. It forms a viscous mass. On drying, it becomes hard and is insoluble in alcohol. Copious amounts of mucilage are present on the leaves and stems of xerophytic plants. The leaves of *Aloe vera* are fleshy due to the presence of great amount of mucilage in the cells. The flowers of *Hibiscus rosasinensis*, fruits of *Hibiscus esculentus* and *Plantago* (Ispagol)

also possess mucilage. These seeds swell up on immersion in water. Mucilage is also secreted by the stem of some water plants. It stains violet with a mixture of iodine and sulphuric acid.

5. **Mineralization.** This is impregnation of various types of minerals in the cell-wall. The chief minerals that are generally deposited are : silica, calcium oxalate and calcium carbonate. The leaves of grasses, wheat, maize and sugarcane, and stems of *Equisetum* have their cell-walls impregnated with silica. Calcium carbonate crystals are deposited in the form of grape-like bunches in the cells of Banyan leaves.

The cell walls of some algae (Cladophora) and fungi are **chitinous** in nature. This is due to the deposition of **chitin**. The process is called chitinization Chitin is absent in the cell-walls of higher plants It is a characteristic substance in the animals and forms the exoskeleton of insects.

ULTRASTRUCTURE OF THE CELL-WALL

As revealed by the electron microscope and X-ray examination the cell-wall seems to contain cellulose blocks measuring 55A° in cross-section and 600A° in length. Each cellulose block is made up of about 60 **cellobiose-units.** Each cellobiose unit is made up of **glucopyranose chains.** Individ[illegible] 33A°² in cross-section. [illegible] **elementary fibrils** or [illegible] micelles [illegible] wide and 600A° long. Twenty elementry fibrils form a **microfibril** which is 250A° on a side and 62,500A°² in area. The elementary fibrils and microfibrils are submicroscopic structures, whereas the [illegible] An aggregation of about 250 [illegible] 0·16μ² in cross-section. They [illegible] ome 1500 fibrils are organised [illegible] fibre must contain in cross- [illegible] glucopyranose chains. The elementary fibrils or the micellae confer a crystalline structure upon the microfibrils. The spaces between the micellae or the intermicellar spaces are about 84A° wide and are filled with water, pectic substances, hemicelluloses, and in the secondary walls these spaces contain lignin and cutin. Occurrence of groups of proteins containing hydroxyproline has also been reported in the intermicellar spaces of primary walls of all the plants. These proteins are thought to serve enzymatic as well as structural functions and are transported to the cell-wall by cytoplasm. Muhlethaler (1967) is *of the opinion* that this protein is involved in the orientation of the fibrils ; whereas Lamport (1955) stated that the protein plays an important role in cell extension.

The micofibrils are variously arranged in the cell walls :—

1. In the primary walls the microfibrils are oriented in a direction more or less transverse to the long axis or even randomly oriented (Fig. 3.6).

2. In the secondary wall there are usually three layers (Fig. 3.7). In the outer layer the microfibrils are crossed into a net-work. In the

middle or second layer of secondary wall the fibrils are almost longitudinally oriented; whereas in the inner layer the orientation is almost transverse.

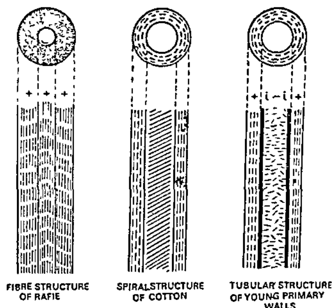


Fig 3 6 Fibrillar orientation in three cell wall types *e g*, Ramie (*Boehmeria nivea*), *Gossypium* and a young primary wall.

3. In the onion root the cell wall of apical initials shows a loosely interwoven mesh of microfibrils. In the slightly older cells the orientration changes to a horizontal pattern. In the elongating cells the pattern changes again to the mesh work type. In the root hair zone the microfibrils are arranged spirally that may be alternately clockwise or anti-clockwise thus resulting in an almost criss-cross arrangement.

4. In the fibre cell-walls of ramie the microfibrils are almost parallel to fibre axis (Fig. 3.6). This condition is not common or typical.

Northcote (19[illegible] cell wall to the [illegible] the growth of th[illegible] and development of the cell wall.

USES OF THE CELL WALL

Cellulose and plastic cell wall materials have been used by Man in diveres forms since antiquity. Ropes made from the fibres of flax and hemp were used by the Stone Age Man, and the linen fabrics were prepared by the Swiss Lake dwellers of the Neolithic. The arts of spinning cotton and flax date back to the Indian and Egyptian civilisations of the third millennium B.C. Refined cotton fabrics were introduced into Europe in fourth century B.C. Other fibres like hemp, jute and ramie were known to the Indian people since ancient times.

The useful natural cellulosic fibres are of diverse origin and include three main types :—

1. **Seed Hairs.** The seed hair products are mainly *cotton* (*Gossypium*), *Salmalia and Ceiba pentandra*. The seed hairs of *Gossypium* contain 85 to 90% cellulose and 6—8% water. Its fibres are 15—35 mm. long and 20—10μ in diameter. They are twisted and flattened single cells. The seed hairs of *Ceiba pentandra* contain 65% cellulose, 12% water and 15% lignin.

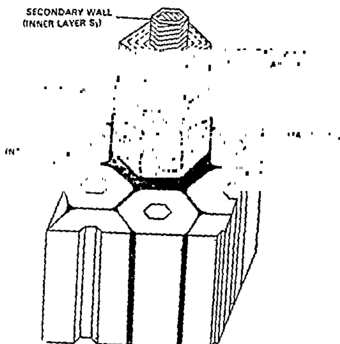


Fig. 3.7. Fibrillar orientation in the primary wall and secondary wall layers of a wood fibre cell. (After Wardrop and Bland).

2. F[illegible]
Corchous [illegible]
(Ramie) [illegible]
65—90% [illegible]
materials. Ramie is notable for the purity of its cellulose. Jute has high lignin content. Flax fibres ar[illegible] in length and 15—20μ in diameter, but the fibres overla[illegible] —90 cm. Hemp gives the fibre lengh o[illegible] ibres may reach upto [illegible] from the bast by [illegible]

3. **Leaf Fib**[illegible]
Agave sisalina (sis[illegible]
cordage and rope-making.

Although native celluloses have retained much of their traditional importance as fibres, recent technological advances have led to the

discovery of several useful derivatives of cellulose *e.g.*, viscose rayon, esters and ethers. Under dehydrating conditions cellulose reacts with nitric acid to yield several nitroesters. The main types include: (*i*) Mononitrates that are used in plastics lacquers; (*ii*) Dinitrates that are used in Lacquers, films and fibres; and (*iii*) Trinitrates that are used in explosives. Among cellulose derivatives, the nitrates have had a long history in fibre and photographic film technology. Celluloids, colloidion and gun-cotton are other important products manufactured from cellulose derivatives.

4

ANATOMY AND TAXONOMY

In the past two or three decades lot of interest has centred around the detailed anatomical study of plants belonging to various families and groups of the spermatophyta. It has resulted in a large number of comprehensive publications on the anatomy of dicots, monocots and even some gymnospermous groups. The work of Metcalf and Chalk, [illegible] Richardson, L.L. [illegible] and MacDeniels, [illegible] D. Pant and his [illegible] needs special mention. The work of A.K.M. Ghouse and Mohd Yunus (1972) on the "Leaf Anatomy in the classification of Indian Conifers" deserves special mention as it marks a significant step towards the identification of conifers based solely on leaf anatomy. The earliar work on the Anatomy of Dicotyledons and various groups of Monocotyledons by Metcalf and Chalk, Tomlinson and D.F. Cutler and a recent work by Prof. K. R. Chowdhry (1966) on the wood anatomy and taxonomy have brought to surface a number of distinct anatomical characteristics that go a long way to enable the taxonomists to identify a particular plant and refer it to its correct taxonomic position. Such detailed studies have also given us sufficient anatomical data to determine the phylogenetic relationships between various taxa. The object of this chapter is to acquaint the students with important anotomical characters that are helpful in taxonomy and phylogeny.

The following are some of the important anatomical characters whose taxonomic value has become well established :—

1. **Hairs.** Recently (1972) Ramayya has classified trichomes in angiosperms on the basis of their structure and development. He divided them into two main categories: **Vegetative** and ***Floral*** trichomes and each category was furthur divided into its own types. His classification has thrown much light on the taxonomic and phyletic importance of the trichomes. He divided the vegetative trichomes, into five phyletic systems (unicellular trichomes, uniseriate filiform trichomes, uniseriate macroform trichomes, *m*-multiseriate trichomes and *p*-multiseriate trichomes) based on ontogenetic and structural differences. The unicellular trichomes, which arise from a single protoderm initial division are of wide taxonomic distribution and

occur in a large number of families. In *Graminae* the unicellular trichomes are quite characteristic and of one type only. They are conical, stiff and pointed at the tip with thin or no contents. They have thick and smooth walls and occur on stem, leaf, ligule, rachis, glumes, lemma and palea and are called the **prickly hair**. In *Clematis gouriana* the unicellular trichomes are of two types : (*i*) **conical type** and (*ii*) **glandular clavate** type. The uniseriate filiform trichomes are small and microscopic and originate by the first periclinal division of the trichome initial. Such hairs are of many shapes and sizes and may be glandular or nonglandular. In *Boerhaavia diffusa*, they are clavate and have robust and much elongated head with uniseriate stalk of cylindrical cells and a unicellular or multicellular foot. The hair cells are filled with a characteristic coloured sap which makes it easy to refer them to the genus. In *Tragus biflorus* (*Gramineae*) the uniseriate filiform hair are pyriform and only two-celled. Many types of this category of hair occur in *Compositae*, *Nyctaginaceae*, *Malvaceae*, *Rosaceae*, *Amaranthaceae*, *Aristolochiaceae*. There are some families which do not possess hair *e.g.*, *Winteraceae*, *Canellaceae*, *Illiciaceae*, *Schizandraceae*, *Trochodendraceae*, etc. In *Theaceae* the hairs are infrequent. In *Himantandraceae* there are found only peltate scales and stellate hair. In *Cercidiphyllaceae* the leaves possess characteristic glandular emergences. Presence of stinging hair, presence of hair with specialised crystals and presence of special types of secretory hair are also characteristics of certain species and are regarded diagnostic anatomical characters. Trichome evidence from some orders (Rosales and Buxales) also throws some light on the polyphyletic origin of Angiosperms (Ramayya, 1972). Cowan (1950) identified many species of *Rhododendron* on account of their trichomes. King and Robinson (1969, 1970) have used the trichome character along with several others in identifying various genera of the *Compositae*.

2. **Stomata.** Florin (1940, 1951, 1958), Metacalfe and Chalk (1950) and Pant (1965) have considered the structure and mode of development of stomata and their spatial relationship with the subsidiary cells as of great taxonomic and phylogenetic importance in the Gymnosperms and Angiosperms. A.K.M. Ghouse and Mohd. Yunus (1972) classified various genera of Indian conifers on the pattern and distribution of stomata. A stoma consists of the guard cells and the pore. The stomata together with the subsidiary cells are usually termed as the stomatal cc [illegible]
shaped (*Zeamays*) [illegible]
In all the grass [illegible]
cells by a thin wall devoid of plasmodesmata or pits. Solereder (1908) classified stomata into four types and gave them family names due to their prevalence in those families *e.g.*, **Cruciferous** type, **Ranuculaceous** type, **Rubiaceous** type and **Caryophyllaceous** type. These types occur in other families also but are abundant in these families *e.g.*, cruciferous type of stomata also occur in *Petunia* and Ranuculaceous type also occur in *Cucurbita* and many other plants, and so on. Recently (1965), Pant and his students have classified stomata on their mode of development :—

(*a*) **Mesogenous stomata.** In them the subsidiary cells have a common origin with the guard cells and develop from the same meristomoid as the guard cells.

(*b*) **Perigenous stomata.** Subsidiary cells do not have a common origin with the guard cells.

(*c*) **Mesoperigenous stomata.** In this type one of the subsidiary cells has a common origin with the guard cells and not with the others.

These different types of st [illegible]
are even characteristics of a [illegible]
taxonomic importance. Sir [illegible]
and his students described 4 types of stomata exemplified by *Allium, Hordeum, Rhoeo* and *Commelina.* They regarded the stomatal type with many subsidiary cells as most primitive. Absence of subsidiary cells is regarded as an advanced character. In the Indian conifers the stomata are generally disposed in parallel rows forming vertical bands on either side of the mid-rib (Ghouse and Yunus, 1972) but in some genera *e.g., Cedrus, Cupressus, Thuja* and *Cryptomeria* the stomata have no regular arrangement. The members of *Pinaceae* that have needle-like leaves, the stomata are found on all the sides of the leaves (amphistomatic). In *Abies, Cephalotaxus, Taxus, Podocarpus, Tsuga* and some other genera, the stomata are **hypostomatic** *i.e.*, are found only along the abaxial epidermis (Ghouse and Yunus, 1972). In *Cupressus, Juniperus* and *Thuja* the stomata are **hyperstomatic** *i.e.*, they are found only on the adaxial epidermis.

3. **Epidermis.** The shape of epidermal cells can, to some extent, be regarded as of some taxonomic value, but one cannot wholly depend upon this character because, similar type of epidermal cells may be present in quite unrelated families. Presence of crystals and other specific chemical substances in the epidermal cells can be regarded as of much importance in taxonomy because these are found only in restricted families. These should, however, not be regarded as indicators of any affinity. Presence of motor or bulliform cells, presence of chloroplasts in epidermal cells and occurrence of vertical and horizontal divisions of the epidermal cells to give rise to a multiple
[illegible] features. Presence
[illegible] pigments
[illegible] tion.

4. **Hypodermis.** The development and distribution of collenchymatous and sclerenchymatous hypodermis can be regarded as an
aid to classification [illegible] continuous or may
occur in patches. [illegible] ted below the
ridges (cucurbitace. [illegible] nchyma may
be angular (*Tagetus* [illegible] or lacunate
type (*Cucurbita*). Sometimes, the sclerenchymatous hypodermis may be made up of sclerides that are again of many types (see chapter on tissues). In the monocots, the hypodermis is quite variable and can be relied upon during identification of generic or even specific level.

Ghouse and Yunus (1972) have successfully used hypodermal variations in the leaves in the classification of Indian conifers. It is absent in *Taxus*, *Cephalotaxus* and *Tsuga* and occurs in distinct patches in *Pinus roxburghii* and *P. merkusii*. In *Abies*, *Cedrus*, *Picea* and *Juniperus*, the sclerenchyma is uniformly distributed. In the leaves of Angiosperms the presence or absence of hypodermis and its distribution can be of great taxonomic importance. Its development and distribution also depend upon ecological features

5. **Veins.** The characters of the veins that can be of taxonomic value include :—

(*a*) The vascular bundles of the veins may be wholly immersed in the mesophyll or raised above the general level of the two epidermal surfaces. The latter condition is quite prevalent among the dicotyledons.

(*b*) The vascular bundles of the veins may be surrounded by a parenchymatous or a sclerenchymatous bundle sheath.

(*c*) Bundle sheath may be one-layered or two-layered. In the latter case both the layers may be parenchymatous or sclerenchymatous or the outer layer is sclerenchymatous and inner layer parenchymatous.

(*d*) The bundle sheath may possess chloroplasts or lack them.

(*e*) Presence or absence of bundle sheath extension. When present, it may be parenchymatous, collenchymatous or sclenchymatous. This character is of generic or even of specific value.

6. **Petiole.** The internal structure of petiole has been regarded as a reliable aid to differentiate between the various taxa because it is, to a greater extent, immune to the ecological factors. Vasculature of the petiole can be taken as a diagnostic taxonomic feature. Care should be taken to examine the sections of the petioles cut at the same level. Metcalfe and Chalk have recognised nine types of vascular structures in the petioles of dicotyledons. Each type may be composed of a single strand or be dissected into a number of bundles according to the species. Identifications at generic and species level can be easily made on account of the vasculature of their petioles.

7. **Crystals.** The various types of crystals of calcium oxalate can also be regarded as aids to taxonomy. The raphides, the sphaeraphides and various other shapes of crystals afford some evidence of their restriction to certain species and help in their identification. Myrosin crystals are very common in *Cruciferae*. Berberin is found in *Berberidaceae*, *Menispermaceae* and *Ranunculaceae*. These families are also closely related. Crystalliferous cells in the partitions between the air lacunae of *Nymphaea* are chararteristic of this genus. In the tribe *Oryzeae*. Tateoka (1963) reported the presence of dumbell-shaped silica bodies in the cells of the veins. This is an important taxonomic character.

8. **Starch.** Starch grains have various shapes that are characteristic of certain plants and sure aids to identification. The starch grains of potato, wheat, maize and rice are quite characteristic and can be safely relied upon for their identification.

9. **Cystoliths.** These are crystals of calcium carbonate and are restricted to certain families *e.g.*, *Urticaceae*, *Acanthaceae*, *Cucurbitaceae*, etc. *Cystoliths of Ficus benghalensis* are quite characteristic of the species. In *Momordica* (*Cucurbitaceae*), the cystoliths occur in groups of 2 or 4 in the epidermal cells.

Crystals of gypsum are present either singly or in clusters in *Tamarix dioica*.

10. **Latex vessels and latex cells.** The latex vessels and latex cells are found only in restricted families *e.g.*, *Euphorbiaceae*, *Papaveraceae*, *Urticaceae*, *Cannabinaceae*, *Compositae*, etc., and their presence can be regarded as a diagnostic character. The colour of the latex and its contents also vary. In *Euphorbia splendens*, for example, the milky latex contains characteristic dumbell-shaped starch grains. Their presence may not indicate affinities as they are found in quite unrelated families. They can only be helpful in identification.

11. **Secretory elements.** The various secretory elements like tanins, mucilages, gums, resins and oils are of great taxonomic importance. The family *Rutaceae* is one of the taxa that possess distinct gland dotted leaves and petals. These organs contain glands that secrete volatile oils. Gum arabica is secretory product of *Acacia arabica*. In *Lauraceae*, the large secretory cells are present that in some species secrete oils and in others mucilage. The morphology of the secretory elements and the chemical nature of their secretions vary with the plants and can be relied upon as distinct characters of taxonomic value. In genus *Tamarix* of *Tamaricaceae* there are found external glands which secrete mineral salts. In certain species of *Ceraria* (*Portulacaceae*) drops of fixed oils are present throughout the stem. Copious mucilage is secreted by almost all the members of the families *Malvaceae* and *Sterculiaceae*. In *Sterculiaceae*, the roots also contain mucilage cells. In *Malvaceae*, mucilage cells, mucilage canals, and mucilage cavities are present in the cortex and in the pith. Secretory glands [illegible] are found in the cortex of *Gossypium*, [illegible] Mucilage canals occur [illegible] and *Thespesia*.

12. **Cork.** The origin of cork cambium, in young stem, has been regarded as of taxonomic value. Its position varies in various families and in various species of the same genus. Its origin may be sub-epidermal and from superficial or deeper layers of cortex and phloem. In the families *Eucommiaceae*, *Winteraceae*, *Cistaceae* and others, the cork arises from the epidermis. In *Cruciferae* the woody species produce cork cambium in the inner part of the cortex and even in phloem *e.g.*, *Arabis precatoreus* and *Aubrietia deltoidea*. Its origin may even vary in the same species with age. Its origin cannot be regarded as a diagnostic feature, but considered along with other characters, it can be regarded as helpful in identification.

13. **Endodermis.** Presence of a distinct endodermal layer in the stems can be regarded as a diagnostic anatomical feature that can be of help in identification, because its occurrence is restricted at least

in the dicotyledons. In *Ranunculacea*, it is not clear in the stem as its cells do not contain either casparian strips or starch grains. In some families the endodermal cells contain starch grains ; whereas in others distinct casparian strips are also present. In some species the endodermal layer becomes suberised.

14. **Pericycle.** The sclerenchymatous elements present generally between the primary cortex and the outer part of the primary phloem are referred to as **pericycle.** In case endodermis is well defined, pericycle is present next to it. The pericycle may be composed of (*i*) an interrupted ring of fibres (*Sunflower, Salvadora, Leptadenia* etc.) ; (*ii*) continuous ring of fibres (*Dianthus caryophyllus, Linum, Cucurbita* etc.) ; (*iii*) interrupted ring of fibres and stone cells ; (*iv*) continuous ring of fibres and stone cells ; (*v*) only made up of stone cells ; and (*vi*) wholly parenchymatous. In the family *Pittosporaceae* sclerenchyma is completely lacking in the pericycle. In *Umbelliferae* it is rare, and in *Geraniaceae* it is present in all the genera and species discovered so far.

15. **Width of Medullary Rays.** Transverse sections through internodes of various plants (primary structures) show varying widths of the medullary rays. In the herbaceous *Ranunculaceae* they are very broad. In *Piperaceae* and herbaceous *Berberidaceae* the bundles are scattered. In *Theaceae* the medullary rays are so narrow that the discreteness of the bundles is not recognisable and xylem appears to [illegible] 's members in *Linaceae* [illegible] whereas some woody [illegible] medullary rays. The width c[illegible] great t[illegible] it as of [illegible] advanced feature as compared to heterogenous ones.

16. **Bicollateral Bundles.** Occurrence of bicollateral bundles *e.g.*, in *Cucurbitaceae*, is of great taxonomic value. Presence of internal phloem is characteristic of some families *e.g., Solanaceae, Asclepiadaceae,* etc.

17. **Anomalous Primary and Secondary Structures.** Presence of cortical and medullary vascular bundles can be regarded as diagnostic features distinguishing families and even genera and species. Scattered arrangement of vascular bundles in dicots (*Piperaceae, Berberidaceae*) and ring-like arrangement in monocots (*Tamus*) is also of great value. Anomalous secondary structures in *Sapindaceae* and *Bignoniaceae* are of great interest.

18. **Wood.** Taxonomic importance of the secondary xylem has also been stressed by Metcalfe and Chalk and Solereder. The presence and absence of vessels, their distribution, diameter perforation, thickening ; types of wood parenchyma (**apotracheal, paratracheal**); width of rays ; kinds of wood fibres (**libriform fibres, tracheidal fibres, septate fibres**) ; storied and non-storied wood ; growth [illegible] presence of **intraxylary phloem,** and chemical nature of the [illegible] substances present in the wood are considered to be useful as

mic aids. Smaller vessels are regarded as an advanced feature as compared to longer ones. Vessels with simple perforations and simple pits are advanced. Similarly, smaller fibres are also advanced.

19. **Bundle Sheath.** Brown (1958) classified grasses into two types: (i) **Festucoid grasses** with a two-layered bundle sheath (*Wheat*); and (ii) **Panicoid grasses** with a single-layered bundle sheath (*Maize*),

Banerji and Swaminathan (1964) were able to utilise anatomical features in grass stems and coleoptiles to distinguish between the various sub-species of *Triticum aestivum.*

Sabins (1921) described the various grasses on the basis of distribution of mechanical tissues in the leaf and stem.

The anatomical similarities between the families *Amaranthaceae, Chenopodiaceae, Nyctaginaceae* and *Phytolacaceae,* which constitute an order **Centrospermales** in Engler's system of classification, do not suggest separation of *Nyctaginaceae* from these families and its inclusion in a separate order, **Thymelaeales** by Hutchinson. The scattered arrangement of vascular bundles in the members of these families suggest a clear relationship between them and the monocots. Maheshwari (1930, p-57) has gone to the extent of remarking "Might not be that such plants represent in some way a transition between the typical dicot and monocot stem organisation by a gradual weakening of cambial activity and scattering of bundles."

Recently (1972), Bocher used anatomical characters to distinguish between three species of *Gymn phyton* (*G. isatidicarpum, G polycephalum* and *G. robustum*). The following table (adapted from Bocher, 1972) shows the differences :—

G. Isatidicarpum	*G. polycephalum*	*G. robustum*
Epidermis		
1. Long axis of the stoma is parallel to the axis of the stem.	1. Long axis of stoma is at right angles to the axis of the stem.	1. Long axis of the stoma is at right angles to that of the stem.
2. Thick stomatal walls are traversed by ectodesmata.	2. Ectodesmata are absent.	2 Ectodesmata are absent.
3 No over-arching of guard cells.	3. Subsidiary cells almost overarch the guard cells forming a shallow extra-point cavity.	3. Subsidiary cells overarch the guard cells.
4. Adaxial part of subsidiary cell outbulges strongly to close the sub-stomatal chamber.	4. There is no such outbulging.	4. Outbulging only slight.

(Contd.)

5. Stomatal pores gradually close by cuticular plugging.	5. Stomata do not close permanently.	5. No permanenr closure of stomata.
Cortex		
6. Sclerenchymatous patches present below the ridges.	6. Collenchyma is present below the ridges.	6. Ridges have collenchymatous bands.
7. Perivascular phellem is formed.	7. No continuous perivascular phellem.	7. No continuous perivascular phellem.
Pith		
8. Small ducts are present in the pith, adaxial to primary xylem.	3 Ducts are absent.	8. Ducts are absent.

Glassman (1972) made a systematic survey of anatomy of taxa of the palm genus, *Syagrus*. He has given an exhaustive key based on anatomical features alone. He has based his key on the anatomical criteria based on the following features as revealed by cross-sections of pinnae alone :—

1. Differences in laminar surface and hypodermis.
2. Frequency and location of various-sized veins.
3. Frequency, shape and location of non-vascular fibres.
4. Size and shape of mid-rib and main vascular bundle.
5. Size and shape of expansion cell tissue.

He has also indicated that leaf anatomy survey of the genus *syagrus* has evolutionary significance because such a survey has unfolded certain sequences which were not apparent by the use of morphological characters alone.

Schmid (1972) has recently employed certain anatomical characters to distinguish between the genera *Eugenia* and *Syzygium*. Besides other differences, the most important and decisive anatomical differences include :—

1. The flowers of *Eugenia* have an interseptal vascular supply to the ovules, whereas in *Syzygium* the supply to the ovules is axile.

2. The architecture of vascular system is closed in the flowers of *Eugenia* as compared to open in the flowers of *Syzygium*.

3. The amount of tannin present in the cells is slight in *Eugenia* as compared to that in *Syzygium*.

4. The amount of Sclerenchyma is none in the flowers of *Eugenia*, whereas in *Syzygium* it varies from slight or none to much.

5. The ovarian tissue is compact in *Eugenia* whereas in *Syzygium* it is spongy.

ANATOMY AND PHYLOGENY

Over a long period of years, taxonomists and systematists have established that there are apparently certain trends in the evolution of the external morphology of angiosperms, especially of the flower. A number of morphological features have been listed to decide the primitive and advanced nature of the taxa. During the last 50—60 years, plant anatomists have worked out the lines of phylogenetic specialisation of the stele, particularly of the secondary xylem. These trends of specialisation have been used to decide the primitiveness or advanced status of a plant or of a family of plants. These trends of specialisation are discussed below :—

1. The **protostele** is primitive, and the **siphonostele** and **dictyostele** are derived. The **eustele** and the **atactostele** are the most advanced states of the stele and are found among the seed plants.

2. In angiosperms the woody stem is primitive whereas the herbaceous stem is derived.

3. Among the imperforate tracheary elements, evolution has advanced from tracheids, to fibre tracheids to libriform wood fibres.

4. There is a decrease in the length of the imperforate elements as they become more specialised *i.e.*, short tracheids and fibres are advanced. The length of cambial initials decreases as specialisation proceeds in the secondary xylem of gymnosperms and dicotyledons.

5. In the angiosperms evolution has proceeded from scalariform tracheids to circular bordered pitted tracheids.

6. The septation of fibre tracheids and libriform wood fibres is a specialised character.

7. The solitary pore arrangement of vessels is less advanced than the aggregate groupings, such as pore multiples, pore clusters, and pore chains.

8. The diffuse porous wood is primitive and the ring porous wood is advanced (Frost, 1930).

9. Vessels with thin walls are more primitive than those with thick walls (Frost, 1930).

10. Vessel elements which are long, small in diameter, and angular in transverse section are primitive than short vessels with large diameter and circular outline in a transverse section (Frost, 1930). As the secondary xylem in gymnosperms and angiosperms becomes more specialised, the cambial initials decrease in length (Arber 1920). The vessel elements, in most cases, are equal to the cambial initials in length (Arber, 1920 ; Chalk and Chhataway, 1933) ; hence the vessel elements also tend to decrease in length.

11. Vessel elements with scalariform perforation plates are primitive than those with a single (simple) opening.

12. Among the vessel members with scalariform perforation plates, the type with numerous bars and narrow perforations is primitive and the type with few bars and wide openings is advanced (Frost, 1930).

13. Vessel elements with long sloping end walls are less advanced than those with transverse end walls (Frost, 1930).

14. Alternate intervascular pitting is advanced as compared to opposite and scalariform types. The latter is most primitive.

15. Spiral thickenings in vessels are indicative of specialisation (Frost, 1931).

16. Homogenous medullary rays are advanced as compared to heterogenous types.

17. The diffuse arrangement of xylem parenchyma is primitive as compared to metatracheal and various paratracheal types.

18. Woods with storied structure are more advanced than woods with nonstratified cells (Arber, 1923).

19. Stomata without subsidiary cells are advanced as compared to those with subsidiary cells (Takhtajan. 1969).

20. Tri-multilacunar node is primitive and the unilacunar node with one trace is advanced (Takhtajan, 1964)

21. Phloem undergoes a series of evolutionary changes comparable to those of the xylem, and, as with xylem, families which are considered to be advanced on other grounds tend to have specialised phloem. Specialised phloem and specialised xylem also tend to go together. The primitive sieve element in angiosperms is long and slender [illegible] forming scattered sieve areas along the [illegible] ry oblique end walls. The sieve elements [illegible] be shorter, with more definite end walls, which come to be perpendicular with the axis. The sieve areas are progressively more restricted to the end walls and more sharply defined, with large pores, and the sieve areas on the lateral walls become obscure or vestigeal. The several sieve areas on the end wall eventually coalesce (phyletically) into a single sieve area. Highly advanced phloem has sieve tubes composed of short sieve tube elements stacked end to end, with each end wall consisting of a single transverse sieve plate with large openings.

22. The sieve elements of more advanced phloem are likely to have two or more companion cells, as viewed in cross section, instead of only one.

23. Primitive angiosperm phloem has a considerable amount of parenchyma intermingled with the sieve tubes and companion cells, but has few or no hard cells. More advanced phloem has little or no parenchyma but has bands of fibres.

Arthur J. Eames (1961) has stated, "The story of evolutionary modification seems to be one of increase in complexity from a simple type, consisting wholly or largely of 'soft cells' to one that has also sclerenchyma cells of one or more types variously arranged, and to a secondarily simple type, consisting largely or wholly of sieve tubes and companion cells"

24. Presence of internal phloem (Bicollateral vascular bundles) is an advanced character. It has, no doubt, originated several times.

25. Stems with scattered vascular bundles as seen in monocots and some dicots are clearly advanced, as compared to stems with bundles arranged in a single ring.

26. Presence of medullary and cortical bundles is also an advanced condition.

Most of these phylogenetic sequences have been worked out by methods which are founded on the work of Bailey and Tupper (1918), Sinnot, Swami, B.G.L., Chalk and Chhataway, Metcalfe and Chalk, Frost, Tippo and Turril and recently by a number of workers (Eames, 1961 ; Esau, 1965 ; Carlquist, 1962 ; Takhtajan, 1959, 1964, 1969 ; Pant and Mehra, 1964 ; Marsden and Bailey, 1955 ; Pant and Gupta, 1966 , Paliwal and Bhandari, 1962 ; Stebbins and Khush, 1961, Parkin, 1953 , and Zimmermann, 1959).

The direction of the lines of specilisation have been established either by founding them on palaeabotanical (Florin 1931), comparative morphological, and developmental studies of all the major vascular plant groups, or, using the work of Bailey and Tupper as starting point, by the methods of association, correlation, exceptions, and sequences listed by Frost (1930, 1931). These phylogenetic trends, therefore, have been formulated independently of any preconceived theories of angiosperm classification ; and any suggestion made by the anatomist may be accepted as evidence obtained by independent methods and thus relatively free of bias. To determine the phylogeny of a group of plants, an attempt is made to harmonize the evolutionary status of the group indicated by the use of the anatomical trends of evolution with the relationship of the group deduced from data obtained from other fields of botany, such as floral anatomy, palaeobotany, cytology, nodal anatomy, embryogeny, pollen morphology, and morphology of the vegetative organs.

5

THE TISSUE

INTRODUCTION

In the preceding chapter, the student has been acquainted with the cell and its marvellous capacities of growth and reproduction. It has also been stated that the division of the cell into two daughter cells is complete only when they are divided by the formation of a middle lamella. This middle lemella, in the multicellular plants, binds the daughter cells together, i.e., it acts as a cementing material. As a result the cells remain bound together and form a multicellular body which may be simple or complex. A peep into the plant world reveals a striking array of simple and complicated forms. The simplest type of plant body is the unicellular type in which the cells separate soon after division or may remain glued together for some time. In such forms the single cell performs all the vital functions of life *i.e.*, it grows, prepares food, undergoes metabolism, reproduces and completes its span of life. The next step towards elaboration is the colonial type of plant body (*Volvox*, *Pediastrum*, etc.) in which a smaller or a larger number of cells live together but perform their own functions or in some cases the functions may be distributed. This is a step towards division of labour. In filamentous forms like *Ulothrix*, we come across a [illegible] differentiation in the cells into a basal holdfast and vegetative cells that also [illegible] like reproduction and growth. Then we come to the *Bryophy*- [illegible] distinct division of labour and differenti- [illegible] *hantia*. *Anthoceros*, *Funaria*). [illegible] ps of mature cells that [illegible] lop chloroplasts and help [illegible] naterial. The former are [illegible] otm the *storage tissue*. So perform their [illegible] in photosynthesis, and another [illegible] *assimilatory tissue*. [illegible] The assimilatory tissue is composed of [illegible] cells or [illegible] the tissues [illegible] a common function *i.e.*, of *photosynthesis*. So a [illegible]

All these cells together pe[illegible] a common function and have a similar origin can group of similar cells that perform a common function and have a similar origin can be conveniently called a *tissue*.

If we look at the higher plants *e.g.*, vascular cryptogams and the spermatophyta, we find that they have highly complex bodies. One or two types of tissues cannot cope with their requirements. A study of their internal structure reveals that they have many types of cells that cluster together to form various kinds of tissues; and two or more types of tissues form tissue systems and the tissue systems form the organs. Each [illegible] performs its particular function, thereby helping a tissue system [illegible] The tissue systems in plants form organs. The [illegible] function well. Let us [illegible] wer and upper epidermis, [illegible] *ascular tissue system* (*Xylem* [illegible] dermal cells, stomata, and [illegible] *ground tissue system* [illegible] and *Phloem*). The epidermal tissue syst[illegible]

hair. Epidermal cells protect the inner tissue, stomata help in gaseous exchange and ...on, etc. ...ue. The ...change. ...former helps in conduction of water and gives support to the organ ; whereas the latter conducts prepared food. In the absence of any of these tissue and tissue systems, the leaf will not be able to perform its function of photosynthesis and transpiration. For example, if xylem is absent, the leaf *will have no support because the thick-walled* xylem elements make up its skeleton. Similar is the case with stems and the roots. In the succeeding chapters we will study in a regular sequence the various tissues, tissue-systems and organs.

This chapter is devoted to the study of a tissue, its kinds, and functions of various types of tissues.

In its broader sense, a tissue may be *defined as a group of similar or dissimilar cells that perform or help to perform a common function, and have a common origin.* The various types of tissues can be conveniently grouped under three headings :

A. **Meristems** or **Meristematic tissue.** B. **Mature** or **Permanent tissue.** C. **Secretory tissue.**

A. MERISTEMATIC TISSUE

A meristematic tissue *is a group of cells that are in a continuous state of division or retain their power of division.* The chief characteristics of the cells comprising a meristematic tissue are :

1. They may be rounded, oval, polygonal or rectangular in shape.
2. They have their walls made up of cellulose.
3. There are no intercellusar spaces between them.
4. The cells do not store reserve food material and are in an active state of metabolism. *They lack crystals and the plastids* are present in proplastid stage. The plastids may be present in the secondary meristems.
5. The cells have abundant protoplasm with numerous small vacuoles or the vacoules may be altogether absent. Some cells of the apical meristems have been reported to contain large vacuoles. Bailey (1930) reported that the cells of cambium are highly vacuolate.
6. They have large nuclei.
7. Th... divide in a particular plane depending upon the positions ... Cambial cells divid... *cells that* give rise ... , at right angles to the surface.

The meristems may be classified as **primary meristems** and **secondary meristems** according to their mode of origin.

Primary Meristems. The meristematic cells that originate from the embryonic stage of the plant, or of an organ of a plant, are classified as **primary meristems.** Such meristems continue to divide or ...ain their power of division and give rise to the primary permanent

tissues of the primary plant body. In some monocots, where secondary growth is absent *e.g.*, palms and banana, the apical portions of the stem are concerned in adding more vascular tissue and thus add to the thickness. It is effected by the activity of embryonic cells of the apex and is, therefore, regarded as primary in nature. Such a meristem is called **primary thickening** [illegible] the primary meristems can be (1) **apical meristems**, (2) [illegible] **meristems.**

1. Apical meristems. These are present at the apices of stems, roots and branches. The activity of the apical meristems adds to the length of the plants or its parts. Two zones can be distinguished in the apical meristems. These are (i) **Promeristem** and (ii) a meristematic zone below it. The promeristem consists of a group of dividing cells called the apical initials. The [illegible] distinguished into three merist[illegible] to the epidermal tissue system [illegible] primary vascular tissue, and (c [illegible] rise to cortex and pith.

2. Inter-calary meristems. As the name indicates these meristems are intercalated in-between the permanent tissues. They may be present either at the base of the internode as in the stems of various grasses and wheat ; or at the base of the leaf as in *Pinus* ; or at the base of a node as in mint (*Mentha* [illegible] stems also add to the length of th[illegible] from the apical meristems when [illegible] growth of the organs. For example, in the grasses when the inter-nodes complete their elongation, some cells at the base retain their meristematic activity and function as intercalary meristems. They lie just above the node.

3. Lateral meristems. These meristems are present along the side of the stem. Vascular cambium in the gymnosperms and the angiosperms is a good example of lateral meristems. The **primary** [illegible] dicotyledenous [illegible] cells, during [illegible] their meristematic activity and function as primary **cambium.** Due to its lateral position it is known as **lateral meristem**. It is always composed of a single layer of rectangular cells that divide only in one plane and produce new vascular tissue on either side. The activity of such a cambium adds to the thickness of the plant.

Secondary Meristems. The [illegible] *that develop from permanent tissues* [illegible] They are not present from the beg[illegible] but develop at a later stage. The [illegible] (healing of wounds) or when [illegible] activity *e.g.*, to effect secondary [illegible] **camb-ium, interfasc**[illegible] cellent examples of se[illegible] tissues

to all these types of secondary ... al in position and are responsible for ... The lateral meritem, primary or secondary, will always give rise to the secondary tissue and bring about secondary growth. The primary growth of the plant is not due to the formation of new cells by lateral meristem. It is effected by the activity of apical and intercalary *meristems*.

B. MATURE OR PERMANENT TISSUES

They are composed of mature cells that, after undergoing complete growth ... size, and function and have ... power of division. The permanent ... may develop thickenings of various degrees and ty... generally living whereas ...
They develop from the ... **tissues**, if derived from apical and lateral meristems or **secondary permanent tissues**, if derived from the lateral meristems. They can be classified into two main types :

(A) **Simple tissues**, and (B) **Complex** or **compound tissues.**

A. SIMPLE TISSUES :

A simple tissue may be defined as *a collection of similar cells that perform a common function*. Simple tissues are classified as :—

(1) **Parenchyma**

(2) **Collenchyma**

(3) **Sclerenchyma.**

1. **Parenchyma** (Fig. 5 ... walled cells. The wall is c... Lignin may be present in ra... possess a distinct nucle... spaces in-between them. These spaces ... conspicuous. The cytoplasm is vacuolat... vary greatly in different plants or in different organs of the same plant. It may be oval, spherical, rectangular, cylindrical, stellate and long spindle-like. They may be variously lobed in the spongy parenchyma of leaves. In the mesophyll of *Xanthorrhoeaceae*, the parenchyma cells have folds and projections (Fahn, 1954). This tissue is generally present in almost all the organs of plants *e.g.*, in roots, stems, *leaves*, *flowers*, fruits and seeds. It constitutes the ground tissue of all the parts of a plant and is generally found in epidermis, cortex, pith, mesophyll of leaves, the pulp of fruits, endoderm of seeds and even in the complex tissues like *xylem* and *phloem*. It is of universal occurrence in all the plants except in undifferentiated lower plants. The meristematic tissues are also made up of parenchymatous cells *i.e.*, thin-walled cells. The chief characteristic of this tissue is that its walls are thin. It originates from the apical meristem of root or stem or from the marginal meristem of the leaves. In the secondary vascular tissues, it is formed by the vascular cambium or even from the cork cambium.

In the water plants, the parenchyma cells in the cortex possess well-developed air-spaces which store air and keep the plants afloat (Fig. 5.1.C). In the land plants the parenchyma cells may be loosely arranged and have intercellular spaces or they may be tightly packed and have few or no air-spaces. The parenchyma in the endosperm of the seeds of various angiosperms lack intercellular spaces.

It may further be classified according to the shape of cells, their contents, and size of intercellular spaces. The shape of cells in ordinary parenchymatous cells is rounded (cortex of the root), polygonal (cortex [illegible] ymatous cells (Fig. 5.1. C) is [illegible] wide air-space between them and may also be called **aerenchyma**. In the cortex of *Hydrilla*, *Potamogeton*, and a number of other plants, the cells in the parenchyma have usual rounded or polygonal shape but leave wide air-spaces for gaseous exchange and also to keep the plant afloat. Such a parenchymatous tissue is also called **aerenchyma**.

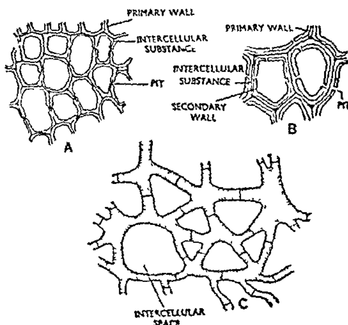


Fig. 5.1. (A—C). Parenchyma. A, Parenchyma cells with primary walls laid down next to the middle lamella. B, Parenchyma cells with secondary walls. C, Aerenchyma from the petiole of *Canna*.

In the leaves the palisade cells are long and contain chloroplasts in them. They help the plant to manufacture its food by photosynthesis and are essentially parenchymatous. Due to their contents,

(chlorophyll) they may be called **chlorenchymatous** or **chlorenchyma** ; due to their palisade-like arrangement they may be called **palisade-parenchyma**, and due to their function, they may be called **photosynthetic** or **assimilatory tissue** In *Lilium* the palisade parenchyma is armed.

Functions. The functions of parenchyma can be listed as under :

(*i*) The main function of the parenchymatous tissue is to store food material in the form of starches, proteins, oils and fats. The parenchymatous tissues in root and stem tubers are good examples The xylem and phloem parenchyma also store starchy food.

(*ii*) The parenchymatous cells (chlorenchyma) that contain chloroplasts are the main seats of photosynthesis *e.g.*, palisade cells of leaf.

(*iii*) In water plants the parenchyma cells have lot of spaces that store air to keep up the buoyancy of the plant. They also facilitiate gaseous exchange.

(*iv*) In the fleshy stems and leaves, the parenchyma cells store water, *e.g.*, *Opuntia*, *Euphorbia sp. Aloe*, etc.

(*v*) Durin [illegible] cells regain their lost activity t[illegible] ot cambium) and help the plant [illegible] th, formation of cork tissue, and healing of wounds. Vegetative propagation by cuttings, layering etc., is due to the meristematic potentialities of the parenchyma cells which divide and develop into buds and adventitious roots. A [illegible] potentialities of the parechyma cells is the [illegible] carrot plant (under experimental condi- [illegible] cells of carrot root.

[illegible] condition they give rigidity to the plant body. If they lose their turgidity, the plant organs droop down. They regain their original position, if the plants are watered.

(*vii*) The various secretory organs of plants are made up of parenchyma cells that secrete various useful products like oils, nectar, resin etc.

2. **Collenchyma.** ([illegible] in possessing localised th[illegible] in the primary body. It [illegible]
It occurs in the stems in the form of two or more layers below the epidermis and forms a layer, called the *hypodermis e.g.*, *Helianthus* and *Cucurbita* In the latter case, it occurs in patches below the ridges It is not found in the roots. It is also met with in the petioles (*Cucurbita*) and along the margins of the leaves. The shape of the cells is generally elongated with oblique end walls. Their length rarely reaches two millimetres. The cells are extensible and possess a considerable degree of plasticity. The ends are rounded or slightly tapering. Majumdar (1941) divides collenchyma into three types. In the hypodermis of *Sun flower* stem, the thickening material is laid [illegible] ells, This type of thickening [illegible] 5.2. B). It is also called [illegible] of *Tagetus*, *Solanum lycopersicum*

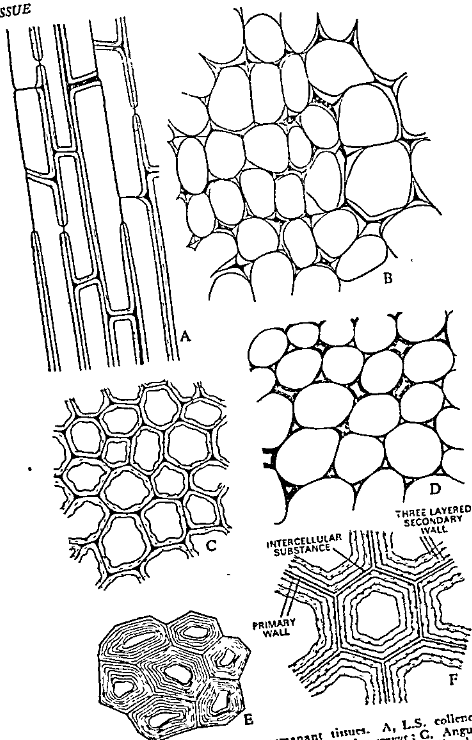


Fig. 5.2. (A—F). Primary permanant tissues. A, L.S. collenchyma ; B, Plate collenchyma from the stem of *Helianthus annuus* ; C, Angular collenchyma from the stem of *Tagetus erectus* ; D, Lacunate collenchyma from the hypodermis of *Cucurbita* stem ; E, Sclerenchyma cells in transection ; F, Sclerenchyma cells with three layered secondary walls.

Datura, *Solanum tuberosum*, *Nicotiana tabacum* and *Atropa belladona*, the thickenings are localised at the angles of the cells. It is called **Angular type** (Fig. 5.2 C). In the hypodermis of *Cucurbita* the thickening material is deposited on the walls bordering the intercellular spaces. This is the **lacunate type** (Fig. 5.2 D). Duchaigne (1955) described **Annular Collenchyma** in which the lumen of the cells is more or less circular in a transverse section. It is stated (Fahn, 1967) that annular collenchyma develops from the angular collenchyma when the latter matures. During maturation, the angular lumen of such cells becomes almost spherical. The thickening material in the cell walls contains high amounts of pectin and hemicellulose. Cellulose is found in smaller amounts. ... tin, 35% hemicellulo ... *Cucurbita* and *Oleand* ... contain chloroplasts and are green in colour ... protoplasm and are ... tances in the thick ... expand and gives a

It is very difficult to ascertain as to whether the collenchyma cells originate from the procambium or from the meristem giving rise to the ground tissue. It is observed that collenchyma originates from elongated cells that resemble procambium and appear in earlier stages of differentiation of the meristem.

Functions. It performs the following functions :—

(*i*) It gives strength to the organs and due to its peripheral position in the stems resists the bending and pulling action of wind. In some leaves the hypodermal tissue is located at the margins of the lamina and saves it from the tearing effect of the wind. Walls of collenchyma cells may become lignified and thick resulting in the formation of sclerenchyma.

(*ii*) It carries on the process of photosynthesis in plants, where chloroplasts are present in the collenhymatous cells.

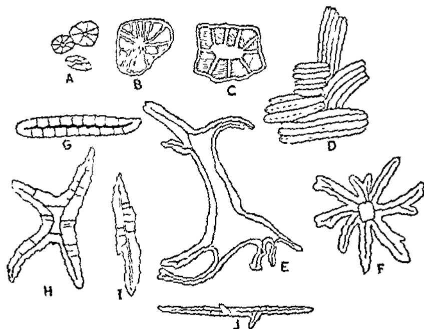
(*iii*) In some plants the collenchyma cells may become thin-walled and regain the power to divide *e.g.*, in those plants where cork cambium develops in the collenchymatous hypodermis.

3. Sclerenhyma (Fig. 6.2 E, F). This type of simple tissue differs from the previous two tissue in possessing thickened secondary walls ... tissue some- ... due to the ... They also ... re generally ... ts. Some of them are longest

Sclereids ... fibres ... sclereids ... fibres ...

sclereids originate from the ordinary parenchyma cells by the addition

of secondary wall layers, whereas fibres originate from meristematic cells and have thus a distinct and predetermined origin. Some of these differences have been challenged by some workers as long sclereids and short fibres have been reported from various sources. Fibres with numerous pits are also known. In *Aristolochia*, the perivascular fibres are converted into stone cells or sclereids during the secondary growth. The continuous layer of perivascular fibres is broken and transformed into groups of stone cells. It is sometimes even difficult to differentiate between parenchyma and sclerenchyma as the xylem parenchyma cells have thick secondary walls. Transitional forms between various types of sclerenchyma cells make a precise classification rather impossible.



F [illegible] A—C Brachysclereids: A, B, from [illegible]

[illegible] called and may be spherical, oval, [illegible] aped, dumbell-shaped (leaf of *Hakea*) or even stellate (leaf of *Nymphaea*). They are generally found in hard parts of plant body and sometimes in the pulp of fruits, like the pear. They can be easily obtained from the hard endocarp of almond and coconut and from the hard seed-coats of some leguminous seeds. They give hardness to the part possessing them. A sclereid has a thick and lignified wall. The thickness of the [illegible] is so much that cavity of the cells (lumen) is [illegible] The thicken- [illegible] laid down at certain parts in the cell wall. [illegible] nt of long and

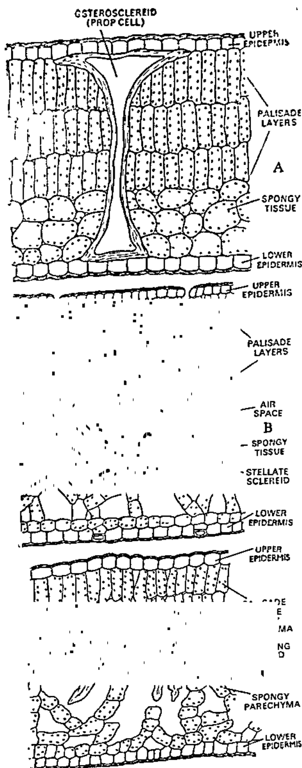


Fig 5 4. Various kinds of sclereids:
A. Osterosclereid in the leaf of *Osmanthus*.
B. Astrosclereid in the leaf of *Nymphaea advena*.
C. Branching sclereid in the leaf of *Trochodendron*.

tubular canals called the simple pits. They may be simple or branched.

Tschirch (1889) classified sclereids into four main types :—

(1) **Brachy-sclereids** or **stone cells** (Fig. 5.3 A—C). Under this category he included the more or less isodiametric sclerieds that are usually found in the bark, pith, phloem, cortex, hard endocarp and fleshy portions of many fruits. Bloch (1926) induced the formation of brachysclereids in the roots of *Philodendron glozioun* by removing the outer layers of cortical cells. Normally, a layer of such sclereids is found a few layers below the epidermis Removal of tissue by experimentation leads to the formation of another such layer in a deeper tissue. Similar brachysclereid formation was induced in the aerial roots of *Monstera delictosa* (Bloch, 1944) by exposing the inner cortical layers to a new environment.

(2) **Macrosclereids** or **rod cells** (Fig. 5.3. D,G). These sclereids have an elongated rod-like shape and are chiefly met with in the outer seed-coat layers of many members of the pea family.

(3) **Ostero-sclereids** or **prop cells** (Fig. 5.4, A). The rod-like sclereids with dilated ends are included under this category *e.g.*, leaf of *Hakea* and leaf of *Osmanthus fragrans*.

(4) **Astrosclereids** (Fig. 5.4, B). Sclereids with stellate form (leaf of *Nymphaea*) are put under this heading.

Bloch (1946) identified as '*trichosclereids* the sclerotic, elongated and hair-like cells in the cortex of the aerial roots of *Monstera deliciosa*. In this case the sclereid cells develop from well-differentiated cells of the cortex parenchyma cells. A row of cortical cells divide vertically to form sclereid initials, which later on elongate and undergo secondary thickening.

The sclereids usually develop from parechymatous cells, which become distinct from other such cells by their larger nuclei and large size. These cells grow considerably and secondary wall is laid down as they mature. These cells then become very thick. The cytoplasm and nucleus later on disappear so that the sclereids are dead cells. In branching sclereids, the enlarging cells grow very rapidly and send out branches into the intercellular spaces between neighbouring cells. In T-shaped sclereids, the sclereid initial sends branches to the neighbouring intercellular spaces, whereas in H-shaped sclereids, the sclereid initial branches into two intercellular spaces. In some cases, the sclereid initial is cubical and sends branches to all the eight corners of the cell. These branches grow into the intercellular spaces and a much-branched sclereid is formed. The final form of the sclereid depends partly upon the disposition and ease of penetration of neighbouring cells. Sclereids present around the veins in leaf mesophyll develop usually from the same meristematic cells that gives rise to the procambial strands.

It is usually believed that sclereids are dead cells but Puchinger (1923), and Alexandrov and Djaparidze (1927) have demonstrated the

presence of nuclei in the stone cells of pulp of *Pyrus* and *Cydonia*, and in some evergreen leaves they have been shown by Puchinger to live one to five years. In *Trochodendron* leaf (Fig. 5.4 C) branching sclereids are present.

(2) **Fibres.** The fibres are sclerenchymatous (thick-walled) cells that form the bulk of mechanical or supporting tissue in the plants. They are found in various organs of the plant and vary in position. In the stem, the fibres may occur in the pericycle, which may be wholly or partially composed of fibres. Such fibres were termed as **pericyclic fibres** in *Cucurbita* because they are not developmentally connected with the phloem. In some cases the hypodermis in the stem may be composed of fibrous cells. In secondary wood, most of the xylem tissue is composed of fibres. The conjunctive tissue or the vascular bundle sheath in most of the monocotyledonous plants is composed of fibres. In leaves of *Nerium*, *Cycas and Pinus* and other xerophytic leaves there is a special hypodermal layer made up of fibre cells. The walls of fibres are lignified, but in some cases *e.g.*, **primary phloem fibres** of some stems, the wall is made up of cellulose. The wall in secondary phloem fibres is always lignified. The fibre cells are generally dead, but may possess some living material in the early stages of their development. The fully developed fibre cells are always dead and are generally long and tapering at the ends. In size they vary between 2—550 mm. in the angiosperms. The length in the gymnosperms varies between 1 mm. and 12 mm. The long fibre, yielding plants are; *Hibiscus cannabinus*, *H. sabdariffa*, *Crotolaria juncea*, *Cannabis*, *Coccos nucifera*, *Linum usitatissimum*, *Corchorus*, *Agave sisiliana*, *Sansevieria*, etc. The walls possess simple and oblique pits and middle lamella is often clearly recognisable.

The fibres are further classified according to their mode of origin and on account of their economic use. They can be classified into three types on the basis of their origin : (1) **Surface fibres,** (2) **Wood fibres,** (3) **Bast fibres.**

1. **Surface fibres.** These fibres are found in the testa of various seeds or from coverings on fruits *e.g.*, cotton fibres (*Gossypium sp.*) *mesocarp* fibres of *Coccos* [illegible] (coconut). The former are used in the manufacture of cloth a [illegible] (*Gossypium negelectum*, *G. arboreum*, [illegible], *G. barbadense*). The latter are hard fibres that are used in the manufacture of ropes, door-mats, etc. Other examples are : *Seiba pentandra* (fibres obtained from pod), *Calotropis procera* (from seeds), *Salmalia malabaricum* (seed fibres). Fibres of these three plants are used as *filing fibres*. The cotton fibres are actually the hair in the seed coat and are not true fibres in the botanical sense.

2. **Wood fibres.** These fibres are present in the xylem of stems and roots (Fig. 5.5). These fibres are also known as *xylary fibres*. They have the same origin *i.e.*, they originate from the derivatives of the cambium, but have varied shapes and can be further classified as (*i*) **libriform fibres** and (*ii*) **fibre tracheids.** These two kinds of

xylary fibres can be differentiated on account of (*i*) the thickness of their walls, the walls in libriform fibres (Fig. 5.5., B) are extremely thick, whereas in fibre tracheids the walls are comparatively thinner ; (*ii*) the libriform fibres have simple pits whereas in fibre tracheids the pits are bordered and ; (*iii*) the length of the aperture does not exceed the diameter of the pit in libriform fibres, whereas it exceeds in the fibre tracheid. The libriform fibres are usually longer than the fibre tracheids. The fibre tracheids should not be confused with the tracheids. The two differ from each other in their length, thickness of walls and

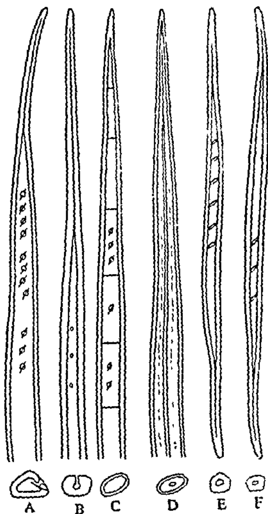


Fig. 5.5. A, fibre tracheid from *Malus pumila*. B, Libriform fibre from *Quercus* sp. C, Septate fibre tracheid from Mahogoni. D, Gelatinous fibre from *Quercus rubra*. E, F. Libriform fibres (*After Eames*).

type of pit chambers. The pit chambers in the tracheids are larger than those of fibre tracheids. Septate fibre tracheids are also known in some plants *e.g.*, *Mahagoni* (Fig. 5.5. C).

maturity but recently (Fahn and Leshem, 1963) xylem fibres in some stems have been shown to contain living contents for several years. The secondary walls are usually made up of lignin, but cellulose is also present in some cases.

Functions of the fibres to the plants The chief function of the fibres to the plant is to give it mechanical strength and their position and distribution in the plant save the plant from the various stresses and strains of the environmental forces *e.g.*, strong wind. Their presence in the leaf gives it rigidity and prevents it from collapsing. Their presence on the surface of seeds and fruits may help in dispersal by wind.

B. COMPLEX TISSUE

A complex tissue or a compound tissue can be defined as *a collection of different types of cells that help in the performance of a common function.* Xylem and phloem are the complex tissues that are found in all the vascular plants. Both these tissues are an assemblage of living and

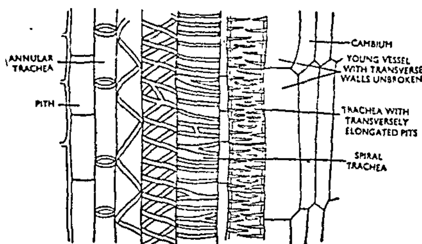


Fig. 5.6. L.S. through vascular bundle showing the various types of cells constituting the xylem tissue. Cambium is also shown.

dead cells and may be primary or secondary, depending upon their mode of origin. The constituent cells of these tissues differ in shape, size and structure, but function in such a manner so as to help in the performance of a function delegated to the tissue.

Xylem

Xylem is a [illegible]
tion of water [illegible]
The primary [illegible]
the growing [illegible] n
are meristematic and are elongated in the longitudinal plane of the organ in which it occurs. The cells have larger nuclei and dense

A third kind of fibre known as *gelatinous fibre* or *mucilaginous fibre* is also known (*Quercus rubra*. Fig. 5.5, D). Such fibres have their innermost wall layer with sufficient a-cellulose which can absorb wate and swell up to form a mucilage that fills the lumen of such fibres. The inner layer of wall is called "G-layer".

3. **Bast fibres.** These fibres can be obtained from the pericycle and phloem of various plants The names of the plants whose pericycle yields fibres are *Cannnabis sativa* (Bhang or hemp) and *Linum usitatissinum* (Alsi or flax). The former is used in the making of ropes, carpets, sacks, paper, twines etc. The fibres obtained from the latter are used in the manufacture of canvas, linen cloth, high quality writing paper etc. The plants yielding fibre from phloem are *Corchorus capsularis*, *C. olitorius* (Jute plant), *Hibiscus cannabinus* (Patsan), *Tilia sp.*, *Eugenia sp.*, *Nerium sp.*, *Calotropis sp.*, *Vinca sp* *Crotolaria juncea* (sun; hemp). Fibres obtained from these plants are used in the manufacture of coarse cloth, cordage, ropes, bags, twines and carpets, etc These fibres are also known as **extraxylary fibres** as they occur outside the xylem. These fibres may form a several-layered tissue usually called pericycle next to the endodermis (*Cucurbita*, *Aristolochia* etc) In monocots they may occur immediately below the epidermis and form a hypodermal layer *e.g.*,. barley. In *Asparagus* they form a many-layered pericycle at a little distance from the epidermis. In maize and other monocots they form a thick-walled sheath around the vascular bundles. In *Nicotiana*, *Nerium*, *Linum*, *Ranunculus*, *Ricinus*, *Corchorus*, etc., they are differentiated from the procambium and are hence a part of the primary phloem. They also occur in the primary phloem of *Gnetum*.

The term **substitute fibres** has been used (Harberlandt. 1918) for certain elongated cells with their walls as thick as those of xylem parenchyma and with living contents They occur in secondary xylem of some plants. Some authors (A. Fahn, 1967) regard them as xylem parenchyma and not as fibres.

Regarding the origin of fibres, they may either originate from the pro-cambium or the cambium or from the ground meristem. The former are present in the vascular tissues (xylem and phloem), whereas the latter occur in the centre. In *Linum e.g.*, the protophloem has small and large cells. The small cells develop into phloem elements, whereas the large cells are young fibres. The fibres in *Cannabis sativa* develop from procambial cells.

Primary fibre cells grow in length with the organ in which they occur. The fibres of *Cannabis* and *Corchorus* (Jute) elongate as the internodes of the stem grow, but may continue to elongate even after the internode has stopped growing. These fibres may thus attain length greater than the surrounding cells. The fibres of ramie (*Boehmeria nivea*) continue to elongate for months together.

Secondary wall is deposited after the fibres have ceased to elongate. Fibres are usually defined as cells that have no living contents at

maturity but recently (Fahn and Leshem, 1963) xylem fibres in some stems have been shown to contain living contents for several years. The secondary walls are usually made up of lignin, but cellulose is also present in some cases.

Functions of the fibres to the plants. The chief function of the fibres to the plant is to give it mechanical strength and their position and distribution in the plant save the plant from the various stresses and strains of the environmental forces *e.g.*, strong wind. Their presence in the leaf gives it rigidity and prevents it from collapsing. Their presence on the surface of seeds and fruits may help in dispersal by wind.

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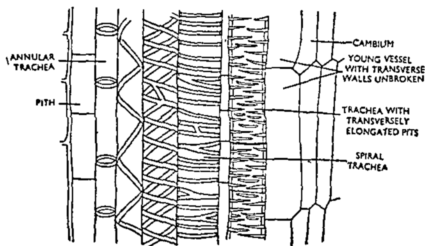


Fig. 5 6. L.S through vascular bundle showing the various types of cells constituting the xylem tissue. Cambium is also shown.

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Xylem

Xylem is a ... the conduction of water ... f the plant. The primary ... iated below the growing ... procambium are meristematic and are elongated in the longitudinal plane of the organ in which it occurs. The cells have larger nuclei and dense

cytoplasmic contents. Its development in the plant is controlled by various factors that are mainly environmental. Ordinarily, it is made up of four kinds of cells (Fig. 5.6) : (1) **tracheids**, (2) **tracheae** or **vessels**. (3) **xylem fibres** and (4) **xylem parenchyma**. This composition of the xylem tissue is extremely clear in the mesophytes and xerophytes. In the water plants (Hydrophytes), it may not show so

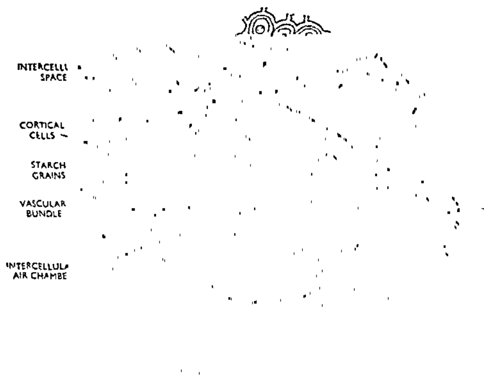


Fig. 5.7. T.S portion of stem of *Elodea canadensis* showing vascular bundle without any differentiation into xylem and phloem and the vascular cells have thinner walls than even the cortical cells.

much differentiation *e.g.*, in *Elodea canadensis*, there is no differentiation of the xylem tissue into four kinds of cells, so much so that it is not possible to differentiate even between xylem and phloem. The xylem or phloem cells in thi
to the cells in the cortex (F
phytes, tracheae are absent.
So this composition of the xylem tissue is not universal, one or the other type of xylem cell type may be absent from the tissue or, as pointed above, there may not be any differentiation at all. In some angiosperms like *Degenaria* and *Drimys* the vessels are also absent. The xylem is called the *primary xylem*, if its elements are derived from the procambium of the apical meristem. *Secondary xylem* elements develop from the vascular cambium during the process of secondary growth.

The earlier formed xylem elements are called **protoxylem**, whereas the later formed are called **metaxylem.**

1. **Tracheids.** These are the characteristic cell types of xylem tissue in gymnosperms and pteridophytes, where they are the chief elements of conduction. They also occur in the primary xylem of some angiosperms (*e.g.*, Magnoliaceae) and are generally present in the secondary wood of the dicotyledonous angiosperms. A tracheid when viewed under the microscope appears to be an elongated cell with tapering ends. In a cross-section the ends may be rounded, chisel-like, or even pointed. In a cross-section the tracheids appear polygonal or rectangular. In a primary xylem they develop or originate from the cells of the procambial strands by the lignification of their walls. The thickening of wall in metaxylem tracheids is generally of the type **bordered pits**. The tracheids in the protoxylem possess annular and spiral type of thickening in the wall. The walls are hard but not very thick and there is a wide cell cavity or the **lumen**. In the pteridophytes and some angiosperms, the bordered pits are

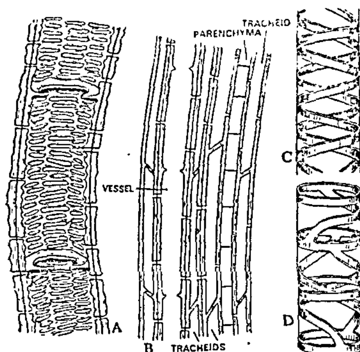


Fig. 5 8. Xylem elements.

A ;

B ;

parenchyma.

C ; Spiral thickening.

D ; Vessel with spiral-annular thickening.

elongated and give a **scalariform** type of thickening. Such bordered pits may be regarded as **scalariform bordered pits** (Fig. 5.8, A). The tracheids form long rows of tracheidal cells placed one above the other The end walls in the tracheids remain in contact and the conduction of water and solutes takes place through the bordered pits present along the end walls. Th... flow of water from tracheid ... minute pores in them. The ... of a valve. They open when t... close when it is unequal. T... when pushed towards one side due to unequal pressure closes the aperture of the pits.

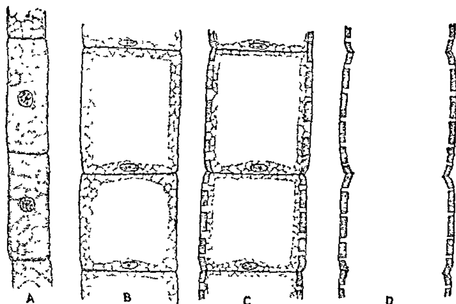


Fig. 5 9. A—D. Various stages in the formation of a vessel.

The xylem elements that develop first from the procambial strands are called **protoxylem elements**, and those that develop later form the **metaxylem elements.**

The tracheids are much smaller than tracheae, rarely exceeding 1 mm. in length, though in some plants they attain a length of 12 cms. or even a metre (some conifers). Isolated tracheids have also been reported in some angiosperms as in *Salicornia*.

The main function of th... their thick and hard walls,

2. Xylem vessels or T... in being cell fusions or *syn*... resorption of the end walls (... of cells, placed one above the other, with their intervening walls (transverse walls) absent (due to dissolution). Such an arrangement of cells in a vessel gives it a pipe-like structure. They can be derived from the tracheids (1) by the dissolution of pit membranes of pits,

which make the end wall perforated, or (2) by the dissolution of entire wall. The length of the tracheae rarely exceeds ten centimetres, though they may attain a length of two metres as in *Quercus*, and 3—6 metres as in *Wistaria* and *Eucalyptus*. The walls of the vessels are lignified and hard, but not very thick. The cell cavity or the *lumen* is wide. The thickenings may be **annular, spiral, scalariform, reticulate** and **pitted**. The protoxylem vessels generally have *annular* (fig. 5.8) and *spiral* (Fig. 5.8) thickenings. The *scalariform* and *recticulate* thickenings develop later by the laying down of more thickening material in the spiral or annular types. The metaxylem vessels generally possess **simple pits** but **bordered pits** can be seen in the vessels of *Tomato*.

The distribution and size of the vessels have been regarded as criteria for classifying the wood into two types :—

1. *Diffuse porous wood* in which the vessels are uniformly distributed throughout the growth layer or the annual ring *e.g.*, *Pyrus*, *Betula*, etc.

2. *Ring porous wood* in which the large vessels are restricted to the early wood and vessels with smaller diameter are restricted to the later formed wood *e.g.*, *Quercus*, *Morus*, etc.

... essels are connect- ... he end wall and ... e above the other. ... simple pore, the perforation plate is called **simple** (Fig. 5.8). In some cases (*Liriodendron*) the perforation plate is **multiple** because it has many pores. If the pores are arranged in a ladder-like manner the multiple perforation is termed as **scalariform** *e.g.*, *Liriodendron*. In *Ephedra* (the only gymnosperm with vessels) the perforations are circular and the perforation plate is called **foraminate**. The perforation plate becomes **reticulate**, if the pores form a network-like appearance. Simple perforation plate is regarded as an advanced type.

In the young and developing vessels the cytoplasm is dense and dictyosomes and endoplasmic reticulum are prominent. Microtubules have also ... ry wall. Aft... yo- somes, en...

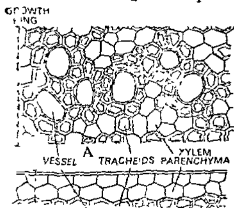
Wood fibres

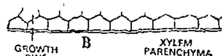
wood fibres can be derived from a tracheid. The fibres that are in a transition stage are spoken of as **fibre-tracheids** (Fig. 5.5. A). During this transition the wall of the tracheid gets thickened and the pits get reduced in size and number, the cell cavity also becomes narrow. The fully developed wood-fibre has only a few pits and a reduced lumen. It is often called **libriform fibre** (Fig. 5.5.) or **typical wood fibre**. Septate wood fibres (Fig. 5.5) have also been reported in some plants *e.g.*, *Mahogony*. A young tracheid with living contents ... forming a ... n

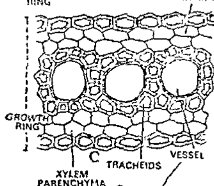
Fibres add to the strength and rigidity of an organ.

4. **Wood parenchyma**. *It is* made of cells with thin walls and living contents. The walls have cellulose. They are present in both primary and secondary xylem. In ... the cells may be ... d ... e ... n-chyma cells in the secondary xylem are generally elongated in a vertical direction. Another type of parenchymatous cells are also present in the secondary xylem. These are ray parenchyma cells. These cells in angiosperms are *radially elongated* and may be helping in radial conduction. According to Chalk and others (1955), the length of secondary wood parenchyma cells remains constant.

The distribution of xylem parenchyma in angiosperm wood *is* variable. Two main types are recognisable :—







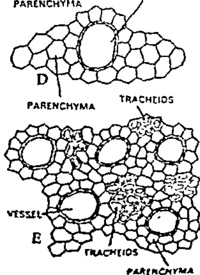


Fig. 5.10. Various types of xylem parenchyma.
A, Diffuse apotracheal type.
B, Terminal apotracheal type.
C, Banded apotracheal type.
D, Vesicentric aliiform type (Paratracheal)
E, Paratracheal-vesicentric confluent aliiform type.

1. *Apotracheal type*. In this case the parenchyma cells are not in contact with the vessels or the two may be slightly in contact. This type may be further classified into three types :

(*i*) Diffuse apotracheal type in which case the parenchyma cells occur singly among the fibres and tracheid (Fig. 5.10, A).

(*ii*) Banded apotracheal type (Fig. 5.10, C) in which the parenchyma cells are arranged in the form of bands *e.g. Hicoria*.

(*iii*) Terminal or boundary apotracheal type (Fig. 5.10. B) in which case the bands of parenchyma are restricted to the ends of the growth rings *e.g., Acer, Saccharum, Michelia* etc.

2. *Paratracheal Type.* In this case the parenchyma cells are definitely associated with the vessels. It can also be sub-divided into the following types :—

(*i*) Abaxial type when the parenchyma cells occur in contact with abaxial surfaces of the vessels *i.e.*, on the surfaces away from the centre of the vessel.

(*ii*) Vasicentric type in which case the parenchyma cells completely surround the vessel. Sometimes, the surrounding parenchyma cells form wing-like extensions (Fig. 5.10, D). Such a type is called ailiform vasicentric type *e.g.*, some Leguminous plants. In *Terminalia* the wing-like extentions of parenchyma around a number of vessels coalesce to form irregular bands. It is called confluent-ailiform vasicentric.

The function of xylem parenchyma or wood parenchyma is to store food material. They may also help in conduction.

So, on the whole, xylems tissue performs two main functions :—(1) conduction ; and (2) mechanical strength.

The advantages of dead tissues in conduction. The tracheids and the tracheae are dead tissues and are chief conducting elements of xylem. These two types of elements die quite early in their development and their death is of great advantage to plants. Water and solutes pass through living cells by osmosis, their rate and direction of movement being independent of one another. Moreover, in living cells the movement is guided by the differentially premeable cell membranes, and also by difference in osmotic pressure in adjoining cells. In the de[illegible] **tracheids** and **tracheae** the water and solutes [illegible] not to diffuse through any diff[illegible] conduction is rapid and [illegible] and cortex of the roo[illegible] of water through a plant [illegible]

Structural advanta[illegible] **of tracheae and tracheids.** The greater length of vessels or tracheae (through dissolution of walls), absence of cross walls, their wider cell cavities, certainly facilitate rapid and

efficient conduction. Tracheids
as compared to tracheae, are,
because they are the only
gymnosperms, which include tl
conifers the conduction is as rapid as in the dicotyledons. Oblique walls have also been regarded as more advantageous as compared to horizontal walls because they afford greater diffusion surface. The term **hadrom** has also been used for conductive part of xylem.

Phloem

The term bast has also been used to denote phloem because the phloem fibres of some plants are used for binding purpose *e.g.*, flax and hemp. The term **leptom** was used by Haberlandt for the conductive elements of phloem (sieve elements). It is a complex tissue made up of four kinds of cells : (1) **Sieve elements,** (2) **Companion cells,** (3) **Phloem fibres** and (4) **Phloem parenchyma.** A fifth kind of cell type has recently been discovered. These are the **transfer cells.** In *Hevea* the phloem is associated with laticifers from which rubber is derived. In *Cinnamomum*, the phloem has oil cells in the secondary state and is, therefore, a source of cinnamon. Like the xylem all these types of cells are not
plant, for example in
ion cells are absent.
tiation into these four types of cells (*Elodea connadensis*). In *Nymphoides peltatum* (Mehta, (1963), the phloem fibres are absent in the primary phloem of the petiole of the leaves. The phloem fibres are also absent in the primary phloem of many other angiosperms. The phloem in the stems is generally present on the outer border of xylem so that both these tissues lie one above the other. In some members of the families. *Solanaceae*, *Compositae*, *Myrtaceae* *Convolvulaceae* and *Apocynaceae*, the primary phloem occurs in small groups internal to the xylem. Such groups of phloem which may or may not be in contact with the xylem elements are called **internal phloem** or **intraxylary phloem.** The elements of this phloem are similar to the external phloem in structure, composition and origin. Of course, they remain primary in nature and are not increased due to secondary growth. Phloem elements derived from the **procambial strands** of the **apical meristems** constitute, **primary phloem** and those that are derived by the activity of the vascular cambium in stems and root is called the **secondary phloem.** The primary phloem elements that develop first from cells of the procambial strands are called **protophloem elements,** whereas those developed later are called **metaphloem** elements. The protophloem elements have narrow calibre and are short-lived. They are crushed by the developing me

—5.18). The sieve elements in the angiosperms, gymnosperms and pteridophytes show slight differences.

In the angiosperms the sieve elements are composed of sieve-cells that are arranged one above the other in distinct linear rows and have sieve-plates ... ed wit ... name ... elements. In the gymosperms and the pteridophytes, the sieve elements have sieve plates on their lateral walls, the companion cells are absent and there is no distinct arrangement of the sieve-cells in linear rows. Such sieve elements are often called **sieve-cells.**

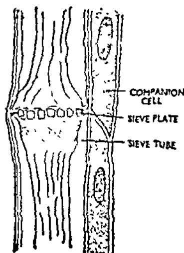


Fig. 5.11. Sieve elements in L.S. (Sieve tube, with sieve plate and companion cells).

The sieve tubes are **syncyst** (formed ... nti- ... ls). ... the ... hly ... The cytoplasm occurs in the form of a thin lining layer along the inner side of the cell walls and encloses a big central vacuole. The nucleus is evident in the younger sieve-elements but disappears in the mature sieve-elements. The vacuole is filled with viscous and albuminous substances that are considered to be proteinaceous in nature ; **leucoplasts** have also been reported to be present in the vacuole. The presence of starchy substance in the vicinity of sieve-plates is attributed to the activity of these **leucoplasts.** A unique feature of the sieve-tube, giving rise to their name, is the presence, at their widest ... transverse sieve plates (Figs. 5.11-6.15). ... *Cucurbita, Nicotiana,* etc.) there is a single ... in the transverse or oblique end wall. In *Vitis vinifera* and some other dicots the end walls of the sieve-tubes are inclined to any extent (Fig. 5.15) and possess several sieve-plates (Fig. 5.15). The sieve plates are the perforated cell walls that are transverse in angiosperms ... phytes. The p... of food materi... in majority of gymnosperms and pteridophytes, they are as fine as the plasmodesmata. The pores in the wide sieve-tubes of many Cucurbitaceae (Fig. 5.14) are very wide and large. In most cases ... In the former, they remain active for a longer period which may extend upto a year or even

more. The cessation of their activities is brought about by a copious amount of deposit of callus on the sieve-plates and their pores.

Developments of Sieve Elements. The sieve-tubes and companion cells develop together from a common mother cell (Fig. 5.18) by its unequal division into a smaller companion cell and a larger sieve

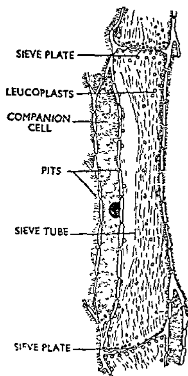


Fig 5.12 *Nicotiana tabacum*. Sieve-tubes with a single sieve plate at the end walls. A companion cell is also shown.

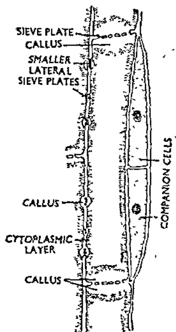


Fig 5 13. *Cucurbita pepo*. A sieve-tube with a single sieve-plate. Callus is also deposited.

cell. Both ... reticulum,
ribosomes,
In *Cucurbit.*
electron microscope,
are presen (Fig. 5.16) in the sieve element. It is sugg...
body is secreted by the endoplasmic reticulum, and is proteinaceous
... ...ections of tubules. It is also
... the differ-
... f P_2 protein
are visibles. In *Cucurbita*, ... me bodies.
The vacuole is quite distinct and is delimited by the tonoplast. In *Pisum sativum* (Figs. 5.16 and 5.17) the sieve elements have numerous microtubules in association with the plasma membrane of the developing sieve-element. During its development the mitochondria undergo

degenerative changes in its inner membrane, which loses its cristae. The chloroplasts if present also degenerate. The slime bodies fuse together to form a mass of slime. It has been observed that at this stage the tonoplast of vacuole ruptures and the vacuolar sap mixes with the cytoplasm forming a substance, called the **mictoplasm** (Engleman, 1965). Sjolund (1968) does not believe in the concept of mictoplasm. At later stages of development the endoplasmic reticulum is replaced

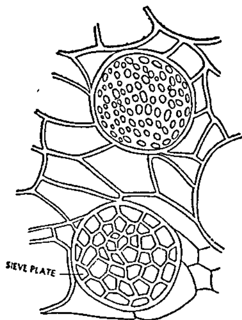


Fig. 5.14. A cross-section showing two sieve-plates. Note the type of perforations (*Lagenerta vulgaris*).

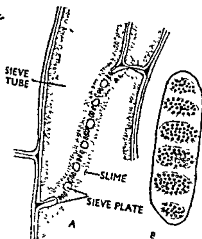


Fig. 5.15. (A—B), *Vitis vinifera*. A, Sieve tube with several sieve-plates on the oblique end wall. B, The end wall as seen in surface view.

by vesicles and the nucleus starts degenerating. It loses its stainability, becomes lobed, the nuclear envelope breaks and the nucleoli are set free into the cytoplasm and ultimately disappear.

The sieve-plate starts developing quite early during the development of the sieve tube. It is quite smooth, when the sieve tube possesses a nucleus *i.e.*, there are no sieve pores. Later platelets of callose develop on the cross wall. These platelets occur on both the sides of the cross walls. In some species (*Pisum sativum*, *Cucurbita*), endoplasmic reticulum may be applied at localised areas on the cross wall. Later platelets of callose appear beneath it. The areas where platelets develop are future sites of sieve-pores. A single plasmodesma appears in each pore site ; the platelets of callose thicken

considerably and later the portion of cell wall between the platelets on either side disappears thus forming a pore. The pore is lined with callose that surrounds the plasmodesmata or the connecting strands. Enzymes are concerned in the process of formation of pores. The

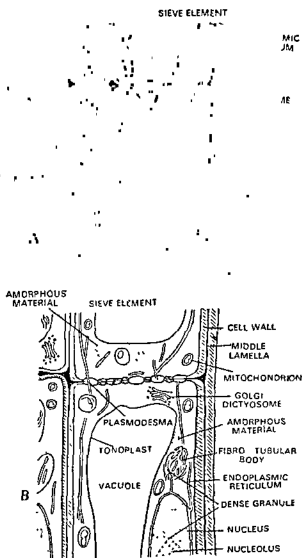


Fig. 5.16. *Pisum sativum*. Structure of phloem under electron microscope. A, younger elements of secondary phloem, sieve-tube along with companion cell. B, A later stage of development. (*After Wark and Chambers*).

connecting strands connect the cytoplasmic contents of the two sieve-tubes lying one above the other. Endoplasmic reticulum has also been seen at pore sites.

The sieve-tubes usually have thick and irregular walls. The thickening is restricted to the lateral walls and does not extend to the sieve plate. The thickening material is quite glistening and the cell-wall is often termed as nacreous.

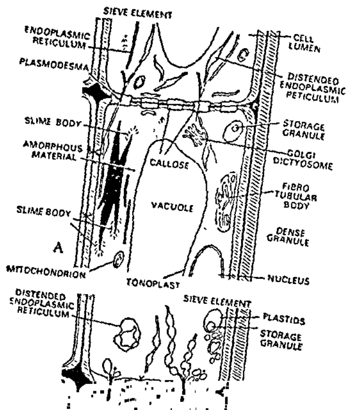


Fig. 5.17. (A—B) Ultra structure of mature elements of secondary phloem of *Pisum sativum*. (*After C.M. Wark and T.C. Chambers.*)

The function of the sieve-tubes is to transmit prepared food material from leaves to other parts of the plant.

2. **Companion cells**. They are characteristic elements of phloem tissue accompanying the sieve-tubes in the angiosperms (both monocots and dicots). They are elements of smaller calibre as compared to the

sieve-tube with which they are associated. In primary phloem the companion cells arise by the unequal longitudinal division of a procambial cell that gives rise to the sieve-tube, (Fig. 5.18). Usually, one companion cell accompanies a sieve tube. There are exceptions also *e.g.*, in Carrot more companion cells than one are attached to the sieve-tube. The ... content wit' ... possess cytoplasmic cellulose. ... hin and made up of ... bodies. They are absent in the pteridophytes and gymnosperms. They are supposed to assist the sieve tubes in the performance of their function of translocation of food. The companion cells and sieve tubes maintain close cytoplasmic connections with each other through numerous fine pits (Fig. 5.12) and plasmodesmata present in their common walls.

3. Phloem Fibres. They are abesent or fewer in primary phloem but are abundant in secondary phloem and are of great economic value. In the primary phloem, their walls have both cellulose and lignified thickenings, whereas in the secondary phloem the thickening is always lignin. The walls have simple pits. There are no living contents and the cell-cavity is narrow. The phloem fibres in the primary phloem are supposed to arise by the crushing of protophloem elements (formed first from the procambial cell). In the secondary

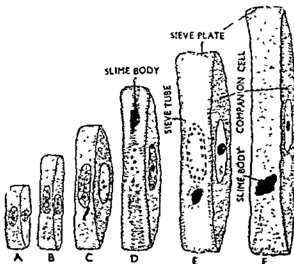


Fig. 5.18. (A—F). Various stages in the formation of sieve-tube and companion cell from a procambial cell. (*After Resch*)

phloem the fibres develop by the thickening of cell walls (sclerosis) of phloem parenchyma of the primary phloem, when it is disorganised due to secondary growth. The chief function of the phloem fibres is to give strength and rigidity to the organ.

The phloem fibres vary in length as well as in the shape of their apices. Their apices may be pointed and needle-like or *blunt* and

obtuse, unilaterally or bilaterally forked or may have teeth-like projections (Liese and Parameswarn, 1972). These various types of apices indicate the presence of intrusive growth in these cells.

4. Phloem Parenchyma. These are parenchymatous cells that are present in the phloem tissue of most of the dicotyledonous angiosperms and pteridophytes. The phloem in monocots and some dicots (some plants belonging to *Ranunculaceae*) do not possess phloem parechyma cells. These cells are with rounded ends and thin cellulose cell walls. The cells possess cytoplasm and nucleus and store food material in the form of starch and fats. They also contain resins and tannins. Phloem parenchyma cells in the secondary phloem are of two types: (1) those elongated in vertical direction, and (2) those elongated in radial direction. The latter are also called *secondary pholem ray cells* and contain lot of stored food in the form of starch, protein and fats. After the cessation of activity of the sieve-tubes, the phloem parenchyma cells get transformed into phloem fibres by the lignification of their wall.

5 Transfer cells. Present techniques, permitting light microscopy of plant tissue sections, coupled with electronmicroscopy, have revealed a special type of cell among the vascular parenchyma in certain situations, frequently adjacent to sieve-tubes. These cells are termed as **'transfer cells'** and are characterised by wall in growths or protuberances and a cytoplasm rich in organelles. They are particularly common in the minor leaf veins of some species of *Leguminosae*. In the leaves of *Pisum*, the transfer cells differentiate at about the same time as export of metabolites from the leaves begins. They fail to develop in the dark. They also differentiate in the cotyledons of several *leguminosae* earlier during germination. Such cells may be specialised for collection of solutes and their transfer to and form the phloem. The interpretation is supported by the observation that similar wall ingrowths are characteristic of the cells of plant glands and haustorial organs *i.e.*, situations where active transfer of solutes occurs.

Conducting tissue in the leaves of some gymnosperms. The leaves, in *Pinus*, *Cycas* and other conifers, do not possess veins. There is only one midrib. In such leaves lateral conduction is effected by a specially developed tissue, called the *transfusion tissue*. In the leaf of *Cycas* this tissue is present around the vascular bundle and extends into the lemina between the palisade cells and the spongy parenchyma. This tissue is made up of two types of cells: (1) *tracheidal cells* and (2) *albuminous cells*. The former are elongated cells with thick and lignified walls, the walls possess bordered pits. The latter are ordinary thin-walled cells that store food material. This tissue in the acicular leaves of *Pinus* is present within the vascular bundle. Here it extends between the xylem and phloem strands and the *endodermis*.

Due to the absence of secondary veins this serves the function of conduction and also gives support to the lamina.

C. SECRETORY TISSUE

There are a large number of plants in the world which have special cells or groups of cells that secrete or excrete products from the plant-body. These tissues are of two main types : (1) **laticiferous tissue** and (2) **glandular tissue.**

LATICIFEROUS TISSUE :

It is found in a large number of plants belonging to the families *Euphorbiaceae, Asclepiadaceae, Papaveraceae, Compositae, Moraceae, Urticaceae, Musaceae* and *Apocynaceae*, etc. The tissue is mainly composed of thin-walled, elongated, branched and multinucleate tube-like structures that contain a colourless, milky, or coloured juice, called the *latex*. They are scattered throughout the ground tissue of the plant and contain stored organic material in the form of starch, rubber, tannins, alkaloids, mucilages, enzymes, proteins, etc. It is further divided into two types · (1) **latex vessels,** and (2) **latex cells.**

Latex vessels, (Fig. 2.26). They are composed of a large number of cells placed end to end with their transverse walls dissolved so as to form long vessels. They originate from the meristematic cells, whose walls get dissolved in the same fashion as in the wood vessels or tracheae. They can be called syncytes. They are unbranched in the beginning, but become richly branched as they grow. A characteristic feature of the latex vessels is that two or more vessels anastomose with each other and their branches fuse with each other forming a net-work. They are found in *Papaver roheas, P. somniferum, Argemone maxicana, Sonchus sp.* (*Compositae*), *Hevea* and *Manihot* (*Euphorbiaceae*), etc.

In poppy (*P. roheas*), the latex contains alkaloids and some injurious narcotics like *Charas* and *Ganja* are prepared from it. In *Hevea* the latex contains rubber which is a hydrocarbon with chemical formula $(C_5H_8)_n$. Latex in *Argemone mexicana* is yellow. In *Musa*, the latex is watery. In this case the latex vessels are unbranched. Roots of *Launea nudicaulos* and *Taraxacum* also contain latex vessels. The cell walls of the latex vessels are thin, and are made up of cellulose. In some cases *e.g., Hevea*, they are thick. The cells are living and the cytoplasm forms a thin lining along the inner sides of the cell walls and contains numerous nuclei. It means that nuclear divisions take place but the cell walls fail to develop. The latex is secreted by the cytoplasm. The latex rapidly coagulates in the air.

Latex cells (Fig. 2.26). They differ from the latex vessels in that they are not formed due to cell fusions and never fuse with other latex cells to form a net-work. Latex cells may be branched or unbranched. They are uninucleate and much smaller in size in the beginning, but as the plant grows they elongate considerably and also show branching. They are as a matter of fact elongated and branched coenocytes. The cell walls are made up of cellulose, the cytoplasm forms a thin layer next to the cell-wall. Cytoplasm is multinucleate, which suggests that

divisions take place but due to the failure of wall formation the cells become siphonaceous and coenocytic. The latex cells can be demonstrated in the following plants : *Calotropis* stem as well as leaf, *Euphorbia splendens*, *Euphorbia tirculli*, *E. neerifolia*, *Nerium odorum*, *Thevetia nerifolia*, *Vinca rosea*, *Ficus benghalensis*, *Ficus religiosa* ; *Cryptostegia grandiflora*, *Daemia extensa*, *Cannabis sativa*, etc. The latex may be milky or colourless or even coloured. The latex in *Euphorbia splendens* and some other species contains rod-like and dumbell-shaped starch grains.

The functions of the laticiferous tissues differ in different plants. They may store food in the form of starch as in *Euphorbia* sp. In some plants like *Nerium* and *Calotropis* it helps to absorb water from adjoining tissue and thus stores it. In some plants *e.g.*, *Papaver roheas* and *Argemone maxicana*, the latex is poisonous and serves to protect the plant against grazing animals. The latex of rubber plant yields rubber of commerce. It is of great industrial importance.

GLANDULAR TISSUE :

As the name indicates this tissue is present in the form of glands in or on various parts of the plant. A gland is a *specialised group of cells that are endowed with the capacity to secrete or excrete products*. The products are secreted by the cytoplasm of the cell and may be stored in the vacuoles of the cells or in a central cavity which may be schizogenous or lysigenous. The cells composing these tissues are generally thin-walled and made up of cellulose, and are living. Their secretions include gums, resins, honey, etc. They are of two kinds : (1) **External glands** (2) **Internal glands.**

1. **External glands.** They generally occur on the epidermal lining of stems and leaves as glandular outgrowths *e.g.*, *glandular hair*, *nectar secreting* and *enzyme secreting glands*.

(*a*) **Glandular hair.** These hair are present in the epidermal layers of leaves and are of various kinds. These may be unicellular or multicellular. The walls of the hair may be thick or thin. They are generally living and possess distinct nuclei. The *stinging hair* (Fig. 8.11, O) present on the under surface of leaf of *Urtica dioca* (Bichhu Buti) are known to most of us. These hair arise from the lower epidermis of the leaf and are unicellular. Their walls are silicified or calcified and brittle. The contents of these hair are poisonous and are secreted by a gland present at the base of the hair. When struck sharply, the hair ruptures obliquely just below its tip leaving a sharp point that pierces the skin like a hypodermic needle. The cell contents, which are in a state of high turgor, rush out and inject an albuminoid poison into the wound, causing lot of irritation that causes blisters on the skin. In *Nymphaea* and *Brasenia schrebra* (Fig. 5.19, B), the leaves possess multicellular mucilage glands that project from the epidermis. Each gland has a multicellular stalk capped by an elongated slime secreting cell. The cell secretes slime or mucilage which encircles the cell and may later on spread along the epidermis. In *Geranium* (Fig. 5.19,A)

and various members of the family *Rutaceae* (orange family), the leaves and the epicarp of fruit possess minute but multicellular projections called *oil glands* or hair tipped with a gland. The hair in this case have a multicellular stalk with a spherical or globular gland at the top. The cells are thin-walled and rich in cytoplasm. The oils secreted by these glands are usually odoriferous (smelling). The oil accumulates in the cell cavity.

(*b*) **Nactaries** or **Nectar-Secreting glands.** Nectaries are special structures that secrete nectar and are present on various organs of flower *e.g.*, petals (*Ranunculus*), in the form of a disc below the ovary (*Rutaceae*), hidden in the spur (*Tropaeolum*), at the base of stamens (*Brassica campestris*), and on the edges of involucre (*Euphorbia pulcherrima*). They are also present on the leaves *e.g.*, at the junction of petiole and leaf blade (*Ricinus*) and on the petiole and lamina (*Passiflora*). Such nectaries are called *extrafloral nectaries*. The former are called *floral nectaries*. The structure of a nectary can be best studied in *Euphorbia pulcherrima*, because these nectaries are sufficiently well developed and bigger in size. The nectaries in this case are composed of a layer of elongated palisade-like cells. The cell walls are thin and the cells are densely filled with cytoplasm and have distinct nuclei. These are secretory cells. They secrete their products directly at the surface. In *Tropaeolum* the nectaries secrete sufficient nectar that drips from the surface and collects in the spur.

(*c*) **Digestive glands** or **Enzyme-secreting glands.**. A few plants (Insectivorous plants) possess the power of digesting proteins from the bodies of insects. This they do by secreting certain digestive enzymes by means of glands or glandular hair. In *Drosera* (Fig. 5.19, C) (sundew)
ally wine-red in colour.
the insects. The hair
icated. There are two
peripheral layers of secreting cells that contain a red pigment. Beneath these layers is another layer of cells called the endodermis. Below the endodermis is a branch of the leaf conductive system (tracheids). *Aldrovanda* and *Dionaea* possess discoid digestive glands on the surface of the leaves. In *Nepenthes* (pitcher plant) digestive glands are present at the base of the pitcher. These are spherical, multicellular structures below which are terminal tracheids of a conducting strand. These glands secrete proteolitic enzymes.

(2) **Internal glands.** There are many plants that possess glands embedded in the various tissues of roots, stems, leaves, flowers and fruits. The roots of *Pinus* possess resin canals in the protoxylem groups. The stems in the members of families *Compositae*, *Umbelliferae*, *Rutaceae*, *Myrtaceae*, etc. possess oil glands. In *Cycas* also there are mucilage ducts that secrete *Sago*. The leaves, fruits, petals of flowers in *Rutaceae* also possess oil glands. The leaves of *Eucalyptus* have glands that secrete aromatic oils and are visible as translucent dots.

In *Citrus sinensis* (orange) (Fig. 5.20) the glands are spherical in shape, each gland has a peripheral layer of thin-walled and living secret-

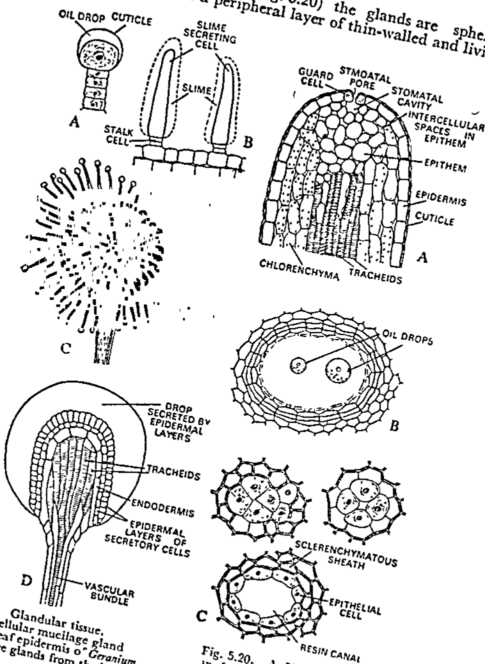


Fig. 5.19. Glandular tissue. A, Multicellular mucilage gland from the leaf epidermis of *Geranium* B, Mucilage glands from the leaf of *Brasenia*. C, Leaf of *Drosera* showing glandular hair. D, Internal structure of a grandular hair of *Drosera* leaf.

Fig. 5.20. A, Hydathode as seen in *L.S* B, Lysigenous oil gland from peel of *Citrus* fruit. C, Stages in the formation of schizogenous resin canal in the wood of *Pinus*.

6

APICAL MERISTEMS

In simplest plants *e.g.*, the lower algae and fungi, the growth is not restricted to a particular region. Any cell can divide and add to the length of the simple plant-body. In such cases there is no apical cell. In higher algae *e.g.*, *Sphacelaria*, *Fucus*, *Dictyota*, etc., the growth takes place by the activity of a cell at the top of the filament (Fig. 6.1). Such a cell is called an **apical cell.** In the *bryophytes*, *ferns* (Fig. 6.2) and most of the *lycopods*, the growth in length takes place by the activity of an apical cell and its derivatives. In some plants and plant groups, growth does not take place by the activity of a single apical cell, but by a group of cells arranged in one or more rows at the tips of roots and shoots *e.g.*, *Lycopodium*, *Angiosperms* and *Gymnosperms*. These layers of cells and their immediate derivatives effect growth of the plant body and give rise to all the types of tissues of the plant body. So the term **apical meristem** is applied to the meristematic initials and their immediate derivatives at the apex of a shoot or a root. *Meristematic initials are those cells that, themselves, remain*

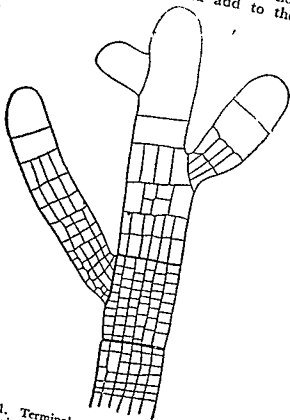


Fig. 6.1. Terminal portion of the alga *Sphacelaria* showing how thallus is produced by the activity of the apical cell and its descendants and how a branch originates.

phenomenon gives the shoot apex an appearance of broad and narrow zones. Schmidt (1924) termed these areas as *maximal* and *minimal* areas of the shoot apex. The time that elapses between the successive initiations of two leaves or pairs of leaves is termed as **plastochoron.**

The size of the shoot apex varies considerably among the spermatophytes. It is 90μ in some grasses and usually varies between 130—200μ in dicots. In banana it is 280μ, in palms it may be 500—800μ (Boke, 1941, Cutter, 1957, Fahn *et al*, 1963). In the Gymnosperms the variations are still great.

The shoot apex has been extensively studied by a number of workers and several theories have been put forward. Gifford (1954) has aptly summarised these theories. Some important ones are discussed in this chapter :—

1. **Apical Cell Theory.** In the year 1759, Wolff recognised the shoot apex and postulated that growth of the plant proceeded from this region of undeveloped cells. Nägeli in 1858 suggested the term **meristem** and put forth an explanation that it consisted of a single cell called **apical cell,** whose activity leads to the development of entire plant-body. It was considered that the plant body in the plants, including the seed plants, arises from a single cell and its derivatives. This theory may hold good for the higher algal groups, bryophytes, and some pteridophytes, but is certainly not applicable to the seed plants. Further investigations have refuted the occurrence of apical cells in all plants and regarded that different parts of plant body arise independently. The apical theory was replaced by the **Histogen theory**.

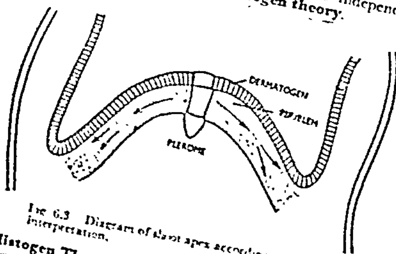


Fig 6.3 Diagram of shoot apex according to Hanstein's interpretation.

2. **Histogen Theory.** It was propounded by Hanstein in 1870. According to this theory, the root and shoot apices of plant consist of a central core called the **'plerome'**. The plerome is surrounded by a variable number of mantle-like layers. These enveloping lay... divided into the outermost layer, called the **'dermatogen'**.

underlying layers (between plerome and dermatogen) called the **'periblem'**. These layers (Fig. 6.3) were designated by Hanstein as the **'histogens'**. He believed that these three layers or the histogens arise from separate sets of **initial cells**, and give rise to tissues : (*i*) the **dermatogen** (from Gre ... gives rise to the epidermis wh ... etimes more than one-layered) ... body ; (*ii*) the **periblem** (from Greek word meaning clothing) gives rise to all the tissues lying between the epidermis and the vascular cylinder *e.g.*, cortex and endodermis ; (*iii*) the **plerome** (from Greek word meaning 'that which fills') gives rise to the entire vascular cylinder including the pith. So Hanstein believed the different regions of the plant body arise from a set of apical initials. *Recent experimentations have,* however, revealed that there is no strict relationship between the development of the histogens and various regions of plant body and the segmentation and layering of the cells in the apical meristem. This theory has the following defects :—

(*i*) There is no distinction into periblem and plerome in the apical parts of many angiosperms and in gymnosperms on the whole.

(*ii*) It is not possible to assign to the histogen the origin of the various regions of plant body as determined by Hanstein.

3. **The Tunica Corpus Theory.** This theory was propounded by Schmidt in 1924 and was developed as a result of increasing attention towards the development and differentiation of shoot apex. This theory recognises only two zones of tissues in the apical meristems. These are (Fig. 6.4) : (*i*) the **tunica,** and (*ii*) the **Corpus.** The tunica designates the layer or layers of cells in the apex in which the pla... point of origin of l... more periphe- ... In ... rpus ... and ... two ... odes ... and are, therefore, undergoing surface growth. The layers ... rpus divide in various directions to add to the volume of the apical ... originate from a separate set of ... 's is equal to the ... has its own layers ... f initials which ... up of derivatives, ... the inner bulk or ... to the Histogen theory, which sets apart three ... periblem, plerome) each of which ... or tissue systems of the *body* ; the ... in any such apical configuration of cells that give rise to distinct tissues below. Except for the *epidermis*

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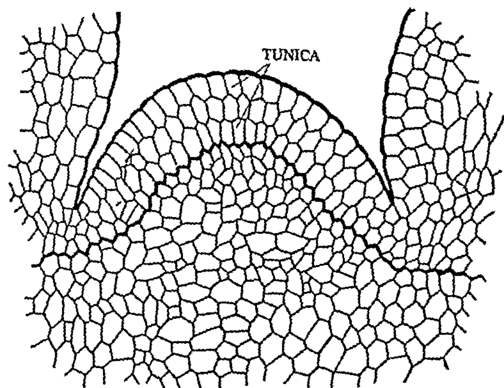


Fig. 6.4. *Vinca minor*. L.S. Through shoot apex, showing three-layered tunica and unlayered corpus beneath it. (*After Schmidt*)

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betw... species at different phases of its ontogeny and (3) in some cases their boundaries are not clear. According to these observations the tunica and the corpus concept has become more flexible and the two regions are treated as morphological entities whose limits are subject to fluctuations and may not be clearly demarcated. In some cases, the number of tunica and corpus layers may be more in the stem apex and less in the branch apex. The innermost layer of the tunica in one part of the plant may ... the outermost layer of the ... peripheral layer ... demarcation ... that derived. If on the other ... the mitosis occur in layers or clusters, the outer ones, if they divide in an anticlinal manner, will form a tunica and the inner ...

There are other theories that have been put forth to explain the apical organisation of the shoot. Dermen (1947) put forth his **Histogenic layer concept.** He did not name any distinct layer of the apical meristems. He did not believe in any terminology and named the different layers of apical meristem as L_1, L_2, L_3, L_4 and so on. These layers were recognized on the basis of their origin. This concept has no support. Popham and Chan (1950) propounded their **Mantle Core Concept.** They used the term **Mantle** for the outer dome-shaped layers that cover the central part, called the **Core.** This is just a substitute of terminology *i.e.*, mantle for tunica and core for corpus. The **Concept of French School** was put forth by Plantefol (1947, 1950), *Buvat (1955) and Amefort (1956). These* authors recognised three distinct regions in the apical meristem. These were designated as **Anneu initial** or the peripheral active zone, **Meristem-ed' attente** or the waiting meristem that becomes active only during formation of inflorescence or terminal flower, and the central region or the **Meristem medullaire.** Newman (1961) put forth his own cencept. He recognised three types of shoot apices :—

1. **Monoplex** type found in ferns and fern allies. The shoot apex may have one or more cells that divide only by walls parallel with the inclined walls in the stem.

2. **Simple**… one or more initial … by anticlinal and …

3. **Duplex** type of shoot apex is found in Angiosperms and consists at least of two successive layers. The surface layer has cells that divide only in an anticlinal manner. The cells in the inner layer or outer layers can divide in more than one plane.

ROOT APEX

A root apex differs from the shoot apex in the following respects :—

1. The root apex is comparatively short and the region of elongation hardly exceeds one millimetre in length.

2. It has no distinction into nodes and internodes.

3. There are no branch primordia in the growing apical region of the root.

4. The lateral roots arise farther back and have endogenous origin (from pericycle).

5. There is present a root cap or calyptra. Due to the presence of root cap, the root meristem becomes sub-terminal in position.

6. There are no leaf-primordia in the root and it is, therefore, devoid of any such changes in shape and activity as are required in the initiation of the leaves.

Due to these differences the root grows uniformly in length and presents no developmental complexities except in some variations

regarding the development of the root cap. The root cap in most of the angiosperms arises from the same initials which give rise to root proper, but in monocotyledons its mode of development is different and independent. The root tip is occupied by actively dividing initial whose activity gives rise to the primary meristematic tissues, which later on give rise to the primary permanent tissues.

The primary meristems, as differentiated from these initials (promeristem) have been divided into three zones by Hanstein. As already described, these zones are called histogens and are named as **dermatogen, periblem**, and **plerome.** Haberlandt (1914) proposed the names **protoderm, ground meristem and procambium.** The ... led ... ses

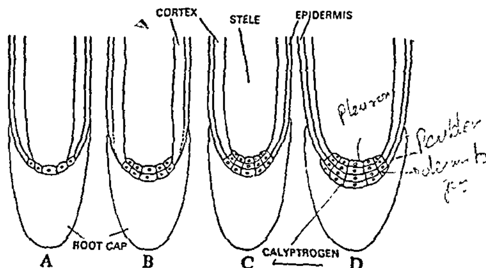


Fig. 6.5. Longitudinal sections (diagrammatic) through various types of root tips. A, Ranalian type. B, Casuarina type. C, typical dicot type. D, Maize type.

Root Apices in Dicots : In the dicots the root apices have been divided into three types, according to the number of initials present at the tip.

... ze some *Legu-* ... which give rise ... the root cap. Some of the cells developing from the root cap differentiate into the epidermis.

2. **Casuarina type**. In the families *Proteaceae, Casuarinaceae*, and some *Leguminosae*, there are two layers of initials at the tip (Fig. 6.5, B). One of them gives rise to the central cylinder and the other to cortex and root cap.

Epidermis arises from the outermost layer of the cortex. In some plants belonging to the families: *Rosaceae*, *Tiliaceae*, *Leguminosae*, and *Juglandaceae*, one of these two layers of initials gives rise to the central cylinder and the inner cortex, whereas the other set of initials gives rise to the outer cortex and the root cap. Epidermis arises from the outermost layer of cortex.

3. **Common type**. In the majority of dicotyledonous families there are three sets of initials (Fig. 6.5, C). Out of these, one gives rise to the epidermis and the root cap, the other to cortex, and the third to the central cylinder.

Root Apices in Monocots. In the monocots four, types of root apices have been recognised.

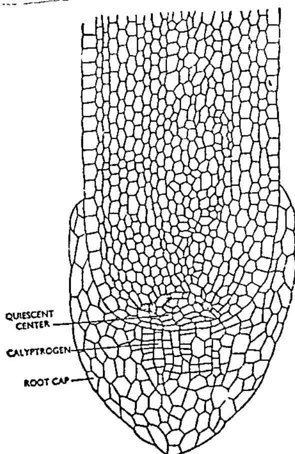


Fig. 6.6. L.S. root tip of *Zea mays* showing the quiescent centre. (*After Clowes*).

The first, second and the third types resemble those described above for dicot roots and are found in *Allium sativum*, *Haemanthus coccineus*, l *Zephyranthes tubispatha*, repectively.

In the fourth type there are four sets of initials, and the root cap, the epidermis, [illegible] origin. The s[illegible] **calyptrogen.** Its activity gives rise to layers of cells towards outside. These layers form a cap-like structure. As the root grows downwards the layers of cap get damaged and new ones are being continuously formed.

The first type of root apical meristem is also found in *Eucharis* and *Amaryllis* (Deshpande, 1960), which have a common initial zone for all the tissues. It is also found in *Allium sativum* and *Aloe vera.* It is very rare.

B.D. Deshpande (1960, 1961) recognises only three types of root apices in the monocots. These are :

1. Cap originates independently and cannot be distinguished into columella (central portion) and peripheral region *e.g., Zephyranthes tubispatha* (Amaryllidaceae), *Sansevieria thyrisifolia, Ruscus hypophyllum* and *Polygonatum oppositifolium* (Liliaceae).

2. "Where cap is distinguishable into columella and the peripheral region, both being independent of each other in histogenesis." He sub-divided this into two types :

(*i*) The peripheral layers of cap are independent of the rest of root tissues and originate from a uniseriate layer. Dermatogen takes no part in cap formation *e.g., Haemanthus coccineus.*

(*ii*) Peripheral layers are distinct but a portion of cap is formed from dermatogen *e.g., Agapanthus* and *Crinum,*

3. It is found in *Aloe vera* and the cap is related to other root tissues and is not independent. There is no distinction into columella and peripherial layers in cap.

Clowes (1956, 1958), while studying the root tips of *Zea mays,* discovered a cap-like region of inactive cells between the root cap and the active meristematic region (Fig. 6.6). He named it as *quiescent centre* whose cells divide rarely and synthesize DNA very slowly as compared to the surrounding cells. B. D. Deshpande (1960—61). studied the root tips of some members of *Amaryllidaceae* and *Liliaceae* and reported the presence of quiescent centre. The function of the quiescent centre is by no means clear, although Clowes has observed that these cells divide during certain periods—particularly during the [illegible] fter the root has been damag- [illegible] "that the quiescent centre [illegible]

Regarding apical organisation two theories have been put forth :—

1. **The histogen theory** (Hanstein, 1968), according to which there are three initiating regions in the root apex (dermatogen, periblem and plerome). These are called **histogens.**

2. **Korper-Kappe Theory** (Fig. 6.7). It was put forth by Schuepp (1917). According to this theory the cells at the root apex divide into two planes. The first division is transverse and one of the daughter-cells then divides by a longitudinal division. The sequence of divisions was called a T-division, because the cell walls form a configuration resembling the letter 'T'. In some zones of the root, especially in the centre, the letter T is erect or straight whereas in other regions of the root the T is inverted, ⊥ (Fig. 6.7). In the former case

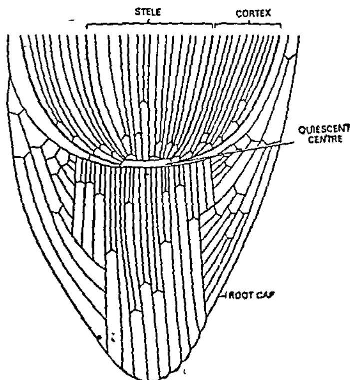


Fig. 6.7. L.S. root apex of *Zea mays* illustrating Korper-Kappe concept.

the bar of the T faces the root apex whereas in the latter case it faces away from the root apex. These two zones of root apex delimited by T and ⊥ were named by Schuepp as **Korper** (body) and **Kappe** (cap) respectively. This theory is comparable with the tunica and corpus theory of shoot apex.

7

HISTOLOGICAL DIFFERENTIATION

The term histological differentiation implies the processes that lead to the differentiation of various tissues of the root and the shoot from their respective apices. In this chapter histological differentiation in the root and the shoot has been considered.

ROOT

The histological differentiation in the root can be conveniently considered under the following headings :—

1. **Organisation of the Root Apex.** The root has a group of undifferentiated cells at its apex. It comprises the **apical meristem** of the primary root. These cells are meristematic and possess the following characteristics :—

(*a*) They have dense protoplasmic contents.

(*b*) Their nuclei are large.

(*c*) They undergo active division.

(*d*) Under electron microscope these cells have been seen to possess small vacuoles.

By various processes of growth and differentiation the cells of the apical meristem give rise to the various tissues of the mature root. Such cells are called the initials. Three types of root apices (Fig. 6.5) have been recognised in the spermatophyta :—

(*a*) Root apices with two layers of initials, giving rise to the vascular cylinder and the other to the epidermis, cortex and root cap. It is the commonest type in the gymnosperms.

(*b*) Root apices with three layers of initial, one giving rise to the cortex, the second to the vascular cylinder and the third to the epidermis and the root-cap.

It is common in the angiosperms.

(*c*) Root apices with three sets of initials that give rise to the ascular cylinder, cortex and epidermis. In such apices the root cap rises from the fourth set of initials known as the **calyptrogen.** This pe is common in the monocots.

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to give rise to the epidermis alone, ... endodermis, whereas the third to the vascular cylinder and the pericycle. This assumption attributes a specific destiny to the derivatives of the three histogens. Such a restricted type of classification is only of descriptive value and is not adhered to strictly in practice and there are variations. The above three types of root apices are also not final and a few more types have been added (for details see chapter six). Modern workers have given the name **promeristem** to this region of apical initials or histogens. The promeristem is, therefore, that part of the root apex which gives rise to all the mature tissues of the root. Recent work has suggested that promeristem is a broad, cup-shaped region of cells situated at the periphery of a central group of inactive cells or the **quiescent centre** (for details see chapter 6).

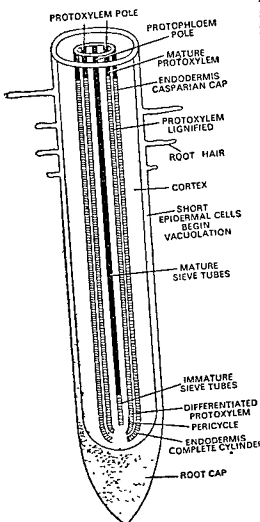


Fig. 7.1. L.S. (diagrammatic) of root tip illustrating various levels of tissue differentiation and maturation proximal to root apex.

2. Tissue Differentiation. The apical initials or the initial cells of the promeristem that lie around the quiescent centre divide periclinally. The inner cells remain meristematic whereas the outer cells by further divisions differentiate into various **tissues** of the root.

The root cap either differentiates from a separate layer of initials or from the same layer of initials that give rise to the cortex or the epidermis. The epidermis, the cortex and the vascular cylinder start differentiating a little behind the root apex. The details of their differentiation are given below.

Epidermis. In some angiosperms and majority of gymnosperms, the epidermis arises from the layer of apical initials that also gives rise to the root cap and the cortex. The layer of initials divides periclinally, the inner remaining meristematic and the outer dividing further to form a few layers, the outermost of which functions as the epidermal layer. In majority of dicots the epidermis arises

from a separate layer of initials that also gives rise to the root cap. In monocots the epidermis arises from a separate layer (dermatogen) which does not give rise to any other tissue. In them the root cap arises

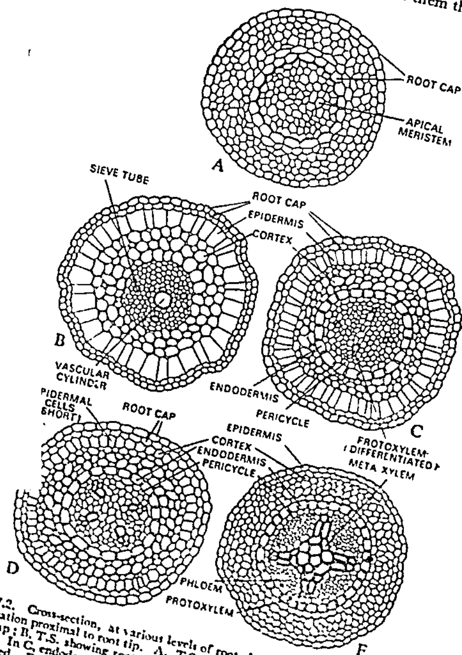


Fig. 7.2. Cross-section, at various levels of root showing tissue differentiation and maturation proximal to root tip. A, T.S. root apex showing apical meristem and root cap; B, T.S. showing root cap, epidermis, cortex and some elements of sieve-tubes. In C, endodermis, pericycles, sieve-elements and xylem elements have also appeared. D—E, represent later stages of development.

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as **exodermis.**

The root hair develop from some epidermal cells in the root hair zone that lies a little distance *from the apical meristem*. They are unicellular and are the tubular outgrowths from the epidermal cells. Presence [illegible] **Trichoblasts** has been reported in the [illegible] and are quite [illegible] abolism. In so [illegible] choblasts develop from the immature epidermal cells (**protoderm**). An epidermal cell divides unequally into two. The smaller cell is the **trichoblast.** It has denser cytoplasmic contents and a bigger nucleus. The *trichoblasts* do not divide further whereas the other cells divide many times. [illegible] DNA and become [illegible] that the nuclei [illegible] ary epidermal [illegible] nuclei in the [illegible] (growth into a root hair).

Cortex. I [illegible] **periblem** [illegible] anticlinally and periclinal [illegible] cortical cells [illegible] arranged with small or large intercellular spaces. In some roots, especially in water plants the cortical cells are regularly arranged in concentric circles.

Endodermis. The innermost layer of cortex differentiates into an [illegible] in structure and [illegible] bolic [illegible] ands on their radial walls. These are thickening bands of suberin. The cells contain enzymes like peroxidase, cytochrome oxidase, polyphenol oxidase and many others. In majority of monocot roots the *suberin* lamella usually develops along the entire inner and radial walls of the endodermal cells. Such thick-walled cells usually develop opposite the phloem elements and spread radially. Some cells, usually opposite the protoxylem elements, remain thin-walled and are called the **passage cells.**

Pericycle. *It is often single-layered and* parenchymatous in the roots. It is derived from the same initials of promeristem that give rise to the vascul [illegible] meristematic activity [illegible] cambium. [illegible]

Vascular Tissues. The vascular tissues differentiate from the **procambium** which differentiates from more mature region of the root towards the root apex (acropetalous). The procambium develops from cells cut off by the root apex initials (promeristem) destined to give rise to the vascular tissue (**plerome**). The procambium cells are meristematic and are filled with dense and granular cytoplasm that is easily stainable and have large nuclei. The cells are elongated in the longitudinal direction of the organ. The cells in the entire central cylinder of the root usually constitute the **procambium**. In some dicots and majority of monocots, the central pith also develops. In this case the portion desired to give rise to the pith is called the **ground meristem**. Progressive tissue differentiation can be conveniently studied in a longitudinal section of the root (Fig. 7.1) or from cross-sections cut at various levels from the root tip (Fig. 7.2). The differentiation of vascular tissue is **centripetal** as opposed to the **centrifugal** differentiation in the stem. The protoxylem starts differentiating at the periphery of the procambial strands which are the first xylem elements to become lignified The metaxylem elements differentiate towards the centre and mature later so that xylem is endarch. The protophloem elements differentiate at alternate radii and appear as angular cells in a T.S. The metaphloem elements appear later next to the protophloem.

The first xylem elements of the root start differentiating about 60 μm from the apex and become mature and lignified at a region proximal to the zone of elongation. The first sieve-elements differentiate at about 180 μm from the root tip and become mature a little beyond the zone of elongation. Experiments have revealed that the distance behind the root apex at which mature xylem and phloem elements mature is variable. It depends upon the rate of growth of the root. It has also been demonstrated exprimentally that hormonal substances, alone or in various combinations, are responsible for controlling the site and amount of cell division in root apical meristem. This also affects the vascular pattern and differentiation. It is also believed that root cap also exerts some control on the vascular pattern in the roots. The number of xylem and phloem strands in the root is probably controlled by the balance between auxin and sugar concentrations. It is not known as to why some elements of procambium differentiate into xylem and others into phloem.

SHOOT

The stem tip is about 0·01 to 0·05 mm. in length and is composed of **primordial meristematic cells** that have very thin walls. These can be regarded as the **initial cells of the shoot.** Next to this is the **zone of determination.** The first distinction between the future cortical, vascular and pith tissues takes place in this zone. In majority of the dicots a group of cells can be distinguished in the **determination zone.** These cells can be made out by special staining methods. In a cross-section these cells are arranged approximately in a circle (see chapter 1, Fig. 1.2). These cells have dense cytoplasmic contents and are designated as a **ring meristem.** The central cells that are **enclosed** by the

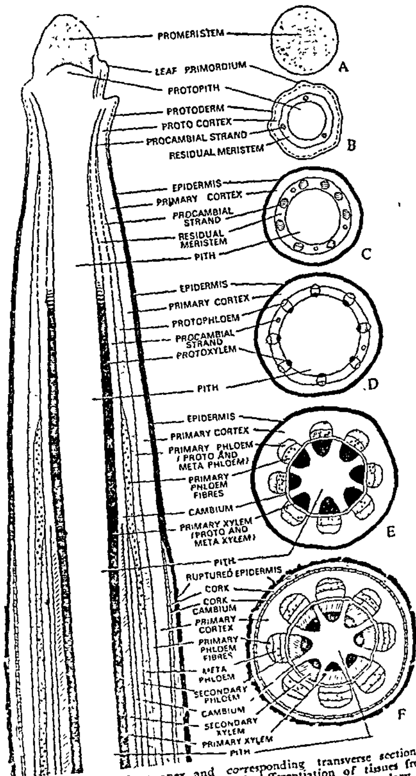


Fig. 7.3. L. S. through shoot apex and corresponding transverse sections of a dicotyledonous plant. It represents a gradual differentiation of tissues from the apex downwards and formation of primary tissues. Beginning of secondary growth is also shown in F.

meristem are designated as the **protopith**. The cells surrounding this ring meristem are called the **protocortex**.

Next to the **determination zone** is the **differentiation zone**, where the different kinds of development patterns prepared in the **determination zone** become visible anatomically. The cells of the **protocortex** and **protopith** start dividing in plane transverse to the longitudinal axis and produce a mass of thin-walled cells that make up the **ground tissue**. The outermost layer of protocortex develops into epidermis.

The cells of the **ring meristem**, nearer to the **leaf primordia** that arise exogenously at the stem tip, divide longitudinally and give rise to groups of elongated, thin-walled cells, which are the future **procambial strands** (Fig. 7.3). The elements of procambial strands differentiate into the primary vascular elements. The distance between the procambial strands, whether they lie close to each other, depends upon the number and size of the **leaf primordia** produced at the apex, as well as the number of the procambial strands forming a leaf trace, a feature, varying from species to species. In case the procambial strands lie close to each other, they may be coming in contact laterally at an early stage, fuse to form a closed or continuous **procambial cylinder** (*Linum*). Such a closed cylinder is perforated for a short distance only at the **leaf** gaps. Such leaf gaps are closed shortly above the departing leaf trace because the **procambium** bordering the gap generates additional procambial tissue which rapidly fills it. The procambial strands adjacent to the cortex differentiate into first phloem elements or **protophloem**. The procambial strands adjacent to the developing pith differentiate to form the **protoxylem elements**. The protoxylem elements have usually spirally thickened walls.

In the seedling of *Brassica campestris* var. *sarson*, the dome-shaped stem apex develops a few exogenous outgrowths a little below it. These develop into leaves. During the earlier stages of the developing leaves, each leaf differentiates five procambial strands. These strands extend down into the stem and form a ring along with other strands (groups of five) from other leaves. These procambial strands, at first, appear as groups of elongated cells. These are continuous with similar groups in the stem. Later, the protoxylem differentiates from the elements of procambial strands lying next to the developing pith. The protophloem differentiates later towards the outer side or the side next to the developing cortex. Sclerenchymatous fibres also appear at the same level and lie outside the phloem. These fibres originate from the external elements of procambial strands if they are associated with the phloem, and from the inner procambial strands, if they are associated with the protoxylem. In *Linum*, the protophloem elements (that differentiate from the procambial strands) possess a mixture of large and small cells, the former are the young fibres and continue to enlarge and develop into long, thick-walled phloem fibres. The smaller cells differentiate into sieve-tubes and companion cells. The same is the

case in *Cannabis sativa* and *Boehmeria nivea*. The young fibres continue to grow with the organ in which they are formed. In *Corchorus*, *Cannabis* and *Boehmeria*, they elongate faster than the surrounding cells. The secondary wall material is laid down after the cells have stopped elongating In *Vitis* and *Zingiber*, the fibres are **septate** and may have living contents. The septa appear after the deposition of secondary wall material on the longitudinal walls.

In some cases *e.g*, *Aristolochia* the sclerenchyma fibres arise in the primary cortex and form a complete cylinder. These sclerenchyma fibres originate from the cells of the **protocortex** or the **ground meristem** by the elongation of certain cells and the deposition of secondary wall-material.

In many stems and leaves *e.g.*, *Cinnamomum, Hoya, Nymphaea, Hakea, Trochodendron, Thea, Olea* etc., specialised cell or cell groups, called the **sclereids** are present They are large and extremely thick-walled and variously-shaped cells, which give mechanical strength to the organ They are randomly distributed and usually develop from the parenchymatous cells. Such cells enlarge in size and possesses larger nuclei. In some cases (*Nymphaea, Hakea, Hoya*), they send outgrowths or branches into the intercellular spaces of neighbouring cells. As they mature, secondary wall material is laid down and they become very thick-walled ; the nucleus and cytoplasm disappear.

In many plants the innermost cell layer of cortex contains large starch grains and is distinguishable as **starch sheath** or **endodermis.** It is one-layered and its cells may develop characteristic thickening strips called the **casparian strips.**

The collateral, open and endarch vascular bundles of plants like *Helianthus annuus*, are differentiated from the **procambial strands.** The vascular elements (xylem and phloem) differentiate within these strands from the two extremities, the differentiation proceeding towards the middle of the bundle of strands. Such a differentiation can be easily studied by cutting serial transvere sections from the stem tip backwards (Fig. 7.3). The protoxylem elements are the first to differentiate from the procambial strands lying a kin to the pith. The vessels differentiate first and have annular and spiral thickenings on their walls. They differentiate from the enlarging cells of the procambial strands that lie one above the other in a row. These cells become vacuolate, the nuclei move to the peripheral layer of cytoplasm. The cells stop enlarging after achieving a certain length. The cross-walls of this row of cells start dissolving and result in the formation of a long tube or pipe, called the **vessel.** The cell walls become thickened by the deposition of secondary wall material in the form of annular or ring-like or spiral bands. The cytoplasm and nucleus disappear. Both the spiral and annular vessels have completed their development, when the surrounding cells are still enlarging and developing or even dividing. These growing cells put a sufficient stretching strain on the mature vessels of the protoxylem. These vessels cannot grow, as they are dead

and are put to a considerable stretching force by the growing cells around them. Their spirally thickened walls enable them to be stretched as they are elastic. Sometimes, they are stretched to such an extent that their walls break down and lead to the formation of a lysigenous cavity (commonly seen in monocot stems). The pitted or scalariform vessels of the metaxylem develop late and are not prone to the stretching force. The cells surrounding them are not increasing in length and have become permanent. The protoxylem has considerable amount of xylem parenchyma. The tracheids and vessels are fewer in number. The xylem fibres are absent in the protoxylem. The metaxylem is composed of tracheids, vessels, xylem fibres and xylem parenchyma. The tracheary elements are wider and well represented. The metaxylem persists even after the primary growth is complete and is destroyed after some secondary growth has taken place. The secondary wall-material in the primary xylem elements is predominantly lignin.

The protophloem differentiates from the **procambial** cells a little below the growing tip. The elements of **protophloem** are fully formed and mature before the surrounding cells of the plant organ complete their elongation *i.e.*, the **protophloem** matures among the elongating cells in the zone of **cell elongation**. Its seive-elements undergo stretching and become disfigured and non-functional. Ultimately, they are obliterated. The **protophloem** elements in the angiosperms consist mainly of **seive-tubes**. The companion cells may or may not be present. The **seive tubes** are narrow and possess **seive plates**. Their protoplast is highly vacuolate. The *sieve tubes* occur singly or in groups among parenchyma cells that may retain their dense cytoplasmic contents and can be clearly differentiated in stained preparations. In some plants *e.g.*, sun-flower, the *sieve-tubes* of *protophloem* occur among greatly alongated parenchyma cells. These elongated cells are considered to be the primordia of the **fibres** and undergo considerable elongation after the obliteration of the **sieve-elements.** They mature as thick-walled fibres and are often designated as thick-walled *pericycle* and **hard bast.** The sclerencymatous portions of the **pericycle** in *sunflower, Aristolochia* and *Cucurbita* are composed of such fibres. Such pericycles form the parts of the vascular tissue and should not be considered as distinct from it.

Metaphloem. In sharp contrast with the **protophloem** the **metaphloem** matures after the surrounding tissue has completed its elongation and growth, and is, therefore, not prone to stretching. It has a longer life, and in lower vascular plants and the monocots (in which there is no secondary growth), and some herbaceous dicots, it is the only food-conducting tissue. It has wider **sieve-tubes** with distinct *sieve-plates.* The **companion cells** and **phloem parenchyma** are present in the gymnosperms and the lower vascular plants. The *phloem* fibres may *metaphloem* of the angiosperms The *companion cells* are absent in the or may not be present. They are usually absent in the *metaphloem* of the dicots. In the monocots, the sclerenchyma fibres usually form a bundle-sheath around the vascular bundles and may also occur in the *metaphloem.*

The perennial monocots such as palms and bamboos, that have no secondary growth, depend mainly upon the metaphloem for their food conduction. *The sieve-tubes in these plants must have a remarkable property to function for several years in spite of the absence of nucleus in their protoplasts.*

The differentiation of the **vascular** tissues in each procambial strand proceeds downwards and inwards towards the centre. A layer of r[illegible] of each bundle. [illegible] cambium [illegible] he formation of s[illegible] s the **vascular** cambium [illegible] the fascicular cambium [illegible]

Root hairs arise from Trichoblast cells

8

THE TISSUE SYSTEM

A group of tissues or a tissue performing a similar function, irrespective of its position in the plant-body, may be regarded to constitute a **tissue system**. The term tissue system does not take into consideration the differences in the structure or arrangement of the cells but is entirely a physiological one. Sachs (1875, pp. 77—109), Haberlandt (1914 pp. 71—72), and Lundergradh (1922, pp. 175) have proposed their own schemes of classification of the tissues in plants. The outline of Sachs' system is given below :

Sachs' Classification. Sachs (1875) recognised three tissue systems in the plants :

1. **Epidermal Tissue System.** It includes the epidermis, cork-layer and various outgrowths from the epidermal cells.

2. **Fascicular Tissue System.** It includes the vascular cylinder and is made up of two complex tissues called the xylem and the phloem.

3. **Fundamental Tissue System.** It is also called the ground tissue system and includes those masses of tissues that have not been included in the first two systems.

In this book, Sach's system is being followed because of its simple frame-work, which can easily be followed by the beginners in plant anatomy. The system is considered to be more suitable by many modern anatomists. It classifies tissue systems according to their topography, development and function.

EPIDERMAL TISSUE SYSTEM

It forms an outermost covering of various organs of plants *e.g.*, young stems, young roots, foliar structures, flowers, fruits and seeds. It is in direct contact with external environment and has to perform manifold functions which are responsible for the structural variations exhibited by this tissue system. The chief functions, performed by this tissue system include *protection*, *absorption*, *secretion*, *excretion*, *gaseous exchange*, *restriction of transpiration*, etc. It will be considered under three headings : (*i*) **Epidermis** ; (*ii*) **Stomata**, and (*iii*) **Various outgrowth from the epidermis.**

1. EPIDERMIS

(Greek *Epi* meaning upon ; and *Derma* meaning skin). It originates from **dermatogen** or the **protoderm**. In case of shoots with distinct **tunica** and **corpus** organisation, the epidermis originates from the outermost layer of the tunica. In roots it originates in different ways (see chapter 6 under root apex) from the root apex, and differs from the epidermis of the shoot in origin, function, and structure. Allen (1947), Linsbauer (1930), and Kroemer (1903), designate root epidermis as **epiblema** or **rhizodermis**. This layer persists as such in plants that do not undergo secondary thickening or have little of it *i.e.*, majority of monocots and herbaceous dicots. In plants which undergo secondary thickening, the epidermis is replaced by periderm. In *Acer striatum*, the epidermis has been reported to remain functional even upto twenty years.

Epidermis is generally uniseriate *i.e.*, it is composed of single layer of epidermal cells whose shape varies with species or in the various organs of the same plant (root, stem, leaves floral organs, seeds, fruits). In some cases the epidermis is composed of several layers of cells *e.g.*, in the leaves of *Ficus elastica*, *Begonia*, *Peperomia* etc. Such an epidermis is called **multiseriate** or **multiple epidermis**. Due to the variety of functions, that this layer has to perform, it is composed of diverse types of cells. In addition to ordinary **epidermal cells**, there are present **guard cells** which guard the stomatal openings, **bulliform** or **motor cells** that are present in many monocot leaves, and various types of outgrowths such as **unicellular** and **multicellular hair, trichomes, glands, mucilage cells** etc.

(*i*) **Epidermal Cells.** They make up most of the epidermis and are compactly arranged They are of varying shapes and sizes, and form a continuous layer, which may be interrupted by stomata. In some cases *e.g.*, petals of some flowers (*Clarkia, Linum*) the epidermal cells are separated here and there by intercellular spaces, which are always covered by cuticle *i.e.*, there is no pore. The epidermal cells are mostly tabular in shape and appear flattened and rectangular in a cross-section In some cases they are isodiametric. In *Aloe aristata*, the epidermal cells in the leaf are hexagonal. In the stem of *Leptadaenia, Salvadora, Calotropis, Capparis decidua*, the epidermal cells are elongated. In the stem of *Anagatis arvensis* the epidermal cells are almost spherical and possess thickened walls, Epidermis in the leaves of *Convolvulus, Sedum, Capsicum, Lycopersicum* etc., exhibits a wavy or an undulating contour when seen in a surface view. The outer walls of the epidermal cells may be flat or convex or may show localised protuberances. The inner walls may be flat or convex or may bear conical projections.

In some members of the families *Graminae* and *Cyperaceae*, the epidermis is composed of two kinds of cells, the **long cells** and the **short cells.** The short cells are again of two types : (*a*) **cork cells**, and (*b*) **silica cells.** The cork cells and the silica cells generally occur in pairs. The former have suberised cell walls, whereas the latter have cells filled with silica (SiO_2). In some plants the epidermis of the root has specialised cells called the **trichoblasts.** The root hair

arise from these cells. These cells have a size and metabolism quite different from the neighbouring epidermal cells.

The epidermal cells are living and retain protoplasmic contents throughout their life. The cells contain a variety of living and non-

divide in response to external stimuli such as wounding and chemical stimulus.

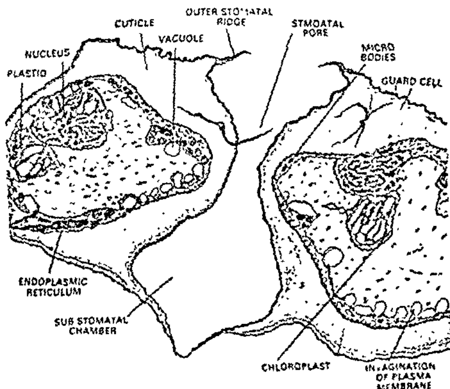


Fig. 8.1. Ultrastructure of Guard cell of *Vicia faba*. (*After James Pallas and Mollenhauer*. 1972)

The walls of epidermal cells vary in their structure and chemical composition. The outer tangential walls of epidermal cells are generally the thickest and the inner tangential walls are the thinnest. The radial walls are thick above and gradually decrease in thickness inwards. Presence of distinct pit pairs and plasmodesmata has also been demonstrated in some plants, that are present on the radial or inner tangential walls. In some plants e.g., *Lonicera japonica*, *Anagalis arvensis*, *Passi-*

is not

y. S

(1914,

p. 402) states that the innermost layers of the outer walls of epidermal cells contain unaltered cellulose. Layers external to this contain varying amounts of cutin.

In addition to the true wall layers of epidermal cells, there is another layer lying external to the outermost walls of epidermal cells This layer is continuous except at the points where stomata occur. This is a separate layer and is made up of a fatty substance called **cutin**. It is a covering layer of all parts of the shoot, including stems, leaves, flowers and even the apical meristems. The active growing regions of the root do not possess cuticle. This layer can be stripped from any part of the plant without breaking it, especially from the lower epidermis of the leaves. The thickness of the cuticle varies in different plants (Figs. 8.2, 8.5) and even in different organs of the same plant. The cuticle has also been observed to extend upto varying depths in the stomatal opening (Fig. 8.5), and sometimes it lines the stomatal chamber *e.g.*, *Musa* and *Ficus elastica* (Fig. 8.5, A). The cuticle has generally a smooth outer surface but in some cases it may be rough and produced into ridges and nodules. In the latter case the epidermal cells are produced into minute protuberances or ridges.

In some plants the cuticle may be coated with wax which may be deposited in the form of granules (plums and grapes), rods (sugarcane), hooked projections, scales or in the form of smooth and homogenous layer. Wax is often deposited in the cutinised layers of the wall and it then becomes almost impermeable to water. Sometimes the wax layer is extended beyond the cuticle forming a light grey bloom, which can be easily wiped off as in the leaves of red cabbage, fruits of plums and grapes. Oils and resins may also get deposited on the cuticle. In *Agave americana* the epidermal cells have thick outer walls which have thick cellulose layer, external to which is a cuticular layer which sends rib-like projections into the cellulose layer, external to this is the cuticle which in turn is covered with a layer of wax grains.

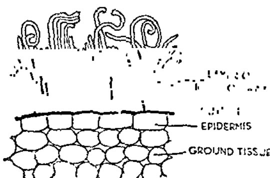


Fig. 8.2. *Saccharum officinarum*. T.S. through nodal regionof stem showing rods of wax.

(*ii*) **Bulliform or motor cells.** Literally, the term bulliform means "bubble-like". These cells are larger in size than the adjacent epidermal cells and have vacuoles. They may be present anywhere in the epidermis or may be restricted in their distribution, and may occur on both the upper and the lower layers of epidermis. These cells are characterised by—

(1) They contain sufficient water and are turgid.

(2) They lack solid contents.

(3) Chlorophyll is either absent or present in meagre amounts.

(4) The cell walls are made up of cellulose and pectic substances. The outer walls are lined with cuticle.

These cells play an important role in unfolding the developing leaves. This is brought about by their sudden expansion. Linsbauer (1930) is of the opinion that they have no other function to perform except to store water. Eames and MacDaniels (1947, p. 338) are of the opinion that these cells bring about rolling of the leaves during dry season. They lose water in dry weather and contract, thus, bringing about rolling of the leaves as in *Poa* and *Ammophila*. By doing so these cells help in reducing the rate of transpiration.

(*iii*) **Multiple or Multiseriate Epidermis.** In some xerophytic leaves *e.g.*, *Ficus elastica*, *Begonia* (Fig. 8.9), *Peperomia* etc., the epidermis is multi-layered. The number of layers in *Peperomia pereskiaefolia* varies from 14—15 layers in the upper epidermis. De Bary (1884) and Guttenberg (1943) regard these subepidermal layers as **hypodermis**. The outermost layer of multiple epidermis resembles the uniseriate epidermis in all respects. It has a layer of cuticle and bears various kinds of outgrowths. In *Begonia* the innermost epidermal layer of the multiple epidermis lacks chlorophyll and functions as water storage tissue. The multiple epidermis saves the underlying tissue from the injurious effects of heat in plants growing in deserts and hot regions. It may also reduce the transpiration rate by preventing the underlying mesophyll cells from heating.

Multiple epidermis originates by tangential divisions of the protodermal cells of the young lamina.

The velamen of the aerial roots is also regarded, by some, as a multiple epidermis meant especially for the function of absorption of moisture from the surrounding air.

2. STOMATA

(Figs. 8.1, 8.3, 8.4, 8.5)

These are minute apertures bounded by two guard cells. They are found mainly in the epidermis of the leaves, and younger parts of the stem. They are absent in the roots and in the aerial parts of some chlorophylless plants like *Monotropa*, *Neottia*. They also occur in the stamens and the carpels. Each stoma can be interpreted as an intercellular space between two highly specialised epidermal cells called the guard cells. In some plants *e.g.*, *Sugarcane* and *Sedum*, the guard cells are bounded by one or more cells that are functionally associated with them and are quite distinct from other epidermal cells. These cells are called the **subsidiary** or **accessory cells**. In the bifacial leaves the stomata generally occur on the lower epidermis, only a few occur on the upper epidermis. In the suberect leaves of m...

he stomata occur on both the surfaces. In the floating leaves *e.g.*, *Nymphaea*, the stomata are found only on the upper epidermis. The position of guard cells in relation to the epidermal cells differs in different plants. They may be at the same level as the neighbouring cells, or they may be slightly raised above them (*Prunus*, *Solanum tuberosum*), or they may be sunken *e g.*, *Musa*. In some xerophytes *e.g.*, *Nerium*, the stomata are present in shallow or deep depressions or

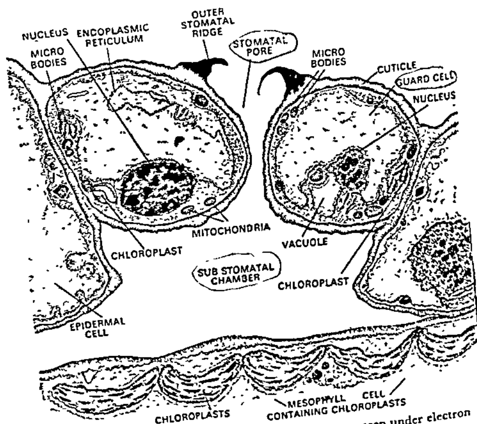


Fig. 8.3. Structure of stoma of *Nicotiana tabacum* as seen under electron microscope. (*After Pallas and Mollenhauer, 1972.*)

crypts in the leaves. In *Nerium* these cavities are lined with unicellular absorbing hair.

The guard cells are living and contain chloroplasts. They are mostly kidney-shaped when viewed from surface and have thick inner wall and comparatively thin outer walls. In maize the guard cells appea dumbell-shaped in surface view. The guard cells generally have pro tuberances of cutin on their upper and lower sides. In a cross-sectio these protuberances appear horn-like (Fig. 8.3). In the leaves of *Pru*

Solanum tuberosum and *Dianthus* (Fig. 8.4), the protuberances are present only on the upper side. In some species of *Pinus* and *Sequoia*, the

Fig. 8.4 Structure of stomata. A, T.S. through stoma of *Ficus elastica* showing cuticle extending into the stomatal opening. B, T.S. stoma of *Dianthus caryophyllus*.

protuberances are absent. The capacity of the guard cells to change their shape and volume, increases or decreases the size of stomatal

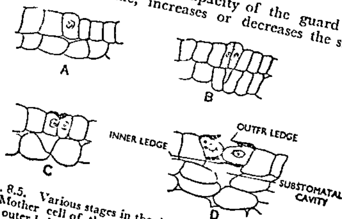


Fig. 8.5. Various stages in the development of a stoma, (A—D). A, Mother cell of the stoma. B—C. Formation of guard cells, and outer ledges. D, complete stoma.

aperture and thus regulates transpiration and gaseous exchange. In
turgid condition the oute
pulled away from the sto
flaccid condition the reve
nishes in size.

James E. Pallas and Hilton (1972) studied the ultrastructure of the guard cells in *Nicotiana tabacum* and *Vicia faba*. (Figs. 8.1, 8.3). They

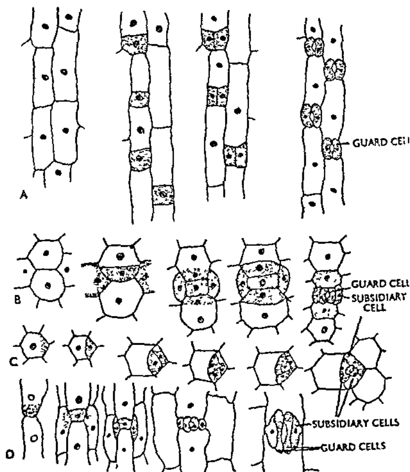


Fig 8.6. (A—D). Development of stomata. A, *Iris* type, B, *Tradescantia* type. C, *Sedum* type. D, *Zea mays* type.
(*After Popham*)

found that the guard cells in both these species contain numerous mitochondria, elements of endoplasmic reticulum, sphaerosomes and some microbodies that appear like **peroxisomes**. The microbodies are bounded by a single membrane. The young stomata have a full ribosomal complement, which, however, is lacking in mature stomata. The guard cells of *Vicia faba* possess lipid droplets external to the plasmalemma. The guard cell chloroplasts of this species are large in size and show a specialised peripheral reticulum. The guard cell

chloroplasts of *Nicotiana* are comparatively smaller in size. Starch is present in the guard cell chloroplasts of both the species. In *Vica faba* the epidermal cell chloroplasts lack starch, but those of *Nicotiana* possess it. Plasmodesmata have been observed between the sister guard cells as well as between guard cells in both the species. The plasmodesmata between guard cells and epidermal cells are found primarily in the pit fields of transverse walls.

The dumbell-shaped stomata in maize have thin-walled swollen ends ; the middle narrow part has thicker walls. In a turgid condition the ends swell and press against each other and the middle portions are pulled apart, thus, causing the stomata to open.

Types of Stomata (Fig. 8.7). Metcalfe and Chalk (1950) classified the stomata, in their adult stage, on the basis of their morphology into the following types.

(i) **Anomocytic type**. In this type the stomata are surrounded by a limited number of cells that are of similar shape, size or form and cannot be distinguished from the rest of the epidermal cells. They have no subsidiary cells e.g., *Cucurbita*.

(ii) **Anisoocytic type**. These stomata are surrounded by three cells of unequal sizes. Two are large and one is smaller e.g., *Petunia*.

(iii) **Paracytic type**. Every stoma is surrounded, in addition to the guard cells, by two subsidiary cells with their long axis parallel to the guard cells e.g., *Phaseolus*.

(iv) **Diacytic type**. The stomata are surrounded by a pair of subsidiary cells. The common wall of the subsidiary cells is at right angles to the guard cells e.g., *Hygrophila*.

Stace (1965) recognised two more types in addition to the above four types : **actinocytic** in which the guard cells are surrounded by four or more subsidiary cells that are elongated radially to the guard cells ; **cyclocytic** in which the 4 or more subsidiary cells are arranged in the form of a ring around the stomata.

(v) **Graminaceous type**. In the members of the families Graminae and Cyperaceae the stomata are dumbell-shaped. They may be surrounded by subsidiary cells which are lying parallel to the long axis of the pore.

Pant (1965) divided the stomata into the following three types :—

1. **Mesogenous type**, in which the subsidiary cells and the guard cells develop from the same mother cell.
2. **Perigenous type**, in which the subsidiary cells develop from the cells lying around the mother cell of the guard cells.
3. **Mesoperigenous type**, in which one of the subsidiary cells has common origin with the guard cells whereas other subsidiary cells have an independent origin.

The above classification is mostly restricted to the dicots.

Stebbins and Jain (1960) recognised four types of stomata in t monocots. These are :—

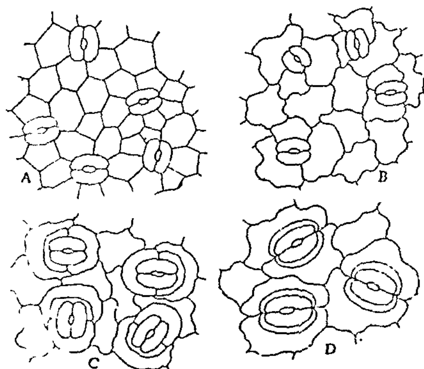


Fig. 8.7. Kinds of stomata in dicotyledons A, Anomocytic stomata from *Cucurbita*. B, Anisocytic stomata from *Petunia*. C, Diacytic stomata from *Hygrophila*. D, Paracytic stomata from *Phaseolus*.

s are not surrounded by ound in *Iris* (Fig. 8.6).

which the guard cells are dumbell-shaped and are surrounded by two subsidiary cells (Fig. 8.6D).

3. **Rhoeo type** in which the guard cells are surrounded by two lateral and two terminal subsidiary cells.

4. **Commelina type** in which the guard cells are surrounded by four lateral and two terminal subsidiary cells.

Stebbins and Khush (1961) regarded stomata with many subsidiary cells as primitive.

Development of Stomata. During the development of a stoma (Fig. 8.6) a young epidermal cell may divide once or several times by anticlinal walls. One of the derivatives of these divisions functions as **a guard mother cell** or **mother cell of the stoma.** This mother cell divides into **guard cells.** The aperture of the stoma is formed by the splitting of the common wall between the guard cells. The surrounding cells of the epidermis may undergo division to form the **subsidiary**

cells. In *Sedum* (Crassulaceae) several divisions take place, in various directions, within a young epidermal cell (Fig. 8.5 C) before the **mother cell** of the **guard cell** originates. These cells which surround the **mother cell** are the **subsidiary cells.** In *Tradescantia* (Fig. 8.5. B) and *Zea mays* (Fig 8.5. D) the subsidiary cells arise by the division of young epidermal cells, which adjoin the stoma.

The function of the stomata is to regulate transpiration and gaseous exchange and, therefore, they play an important role in the vital phenomenon of respiration and photosynthesis.

Recently, Aylor, Parlange and Krikorian (1973) have suggested that certain anatomical features of the guard cells are responsible for their opening and closing mechanism. They have demonstrated these results by means of models Von Mohl (1856) and Schwendener (1881) regarded assymmetrical thickening of the guard cell walls as the basis of stomatal opening and closing, especially in those cases in which a bending of the guard cells occurs. Schwendener stated that the thickness of the ventral wall (*i.e.* next to the pore) is responsible for the bending of the guard cell when pressure increases within the cell. These observations have been supported by many recent authors like Esau (1965), Heath (1959), Stalfelt (1956) and Meidner and Mansfield (1968). Ziegenspeck (1938, 1941, 1955) showed that the cellulosic microfibrils in the guard cell walls are arranged radially from the central aperture to the dorsal wall and may play some role in the opening and closing of stomata. Vaihinger (1942) was the first to challenge the necessity of unequal thickening of guard cell walls for opening. He regarded the presence of thickened ridges only a protective measure. Aylor and his co-workers (1973) have proved that the orientation of cellulosic microfibrils in the guard cell walls is the crucial feature without which stomata would not open. They have shown that thick ventral wall of the guard cells is not necessary for opening and is rather a hindrance to the opening mechanics.

3. Epidermal Outgrowths

These will be considered under two headings :—

A. Trichomes

B. Root hair

A. **Trichomes** (Greek, growth of hair). This term is used to designate various unicellular and multicellular appendages that originate from the epidermal cells. They are found on almost all plant parts and may be permanent or temporary features. Some of them remain alive throughout their existence on the epidermis, whereas some of them lose their protoplasmic contents and occur as dried structures. Foster (1949, pp. 72—74) classifies them into 4 main categories (*i*) *Hair* ; (*ii*) *Scales*, (*iii*) *Colleters* ; and (*iv*) *Water vesicles* or *bladders*.

Ramayya, N. (1962, 1972) proposed a different classification of the trichomes of angiosperms. This classification is based on the ontogeny of the trichomes. It is given below in tabulated form :—

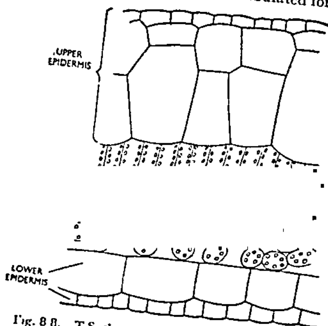


Fig. 8.8. T.S. through the leaf of *Begonia* showing three-layered upper epidermis and two-layered lower epidermis. In-between the two is a centrally placed chlorenchyma, consisting of one-layered palisade tissue and many-layered spongy tissue of loosely arranged cells.

omes

I. Vegetative Trichomes

1. *Unicellular trichomes.* They are of wide occurrence and may be glandular or nonglandular and variously shaped.

2. *Uniseriate filiform trichomes* that are multicellular and uniseriate wholly or in part, with first division of the trichome initial periclinal e.g., *Malvaceae, Rosaceae, Compositae*, etc.

3. *Uniseriate macroform trichomes*, that are as in No. 2, but are large and robust and have vacuolate contents.

In this text Foster's classification is followed :—

(i) **Hair.** The hair can be classified as :

(a) *Unicellular hair*. The unicellular hair may be long and coiled or short and may be branched or unbranched. The unicellular hair from the stem of *Gossypium arboreum* (Fig 8.9, B) are long and thick-walled. The unicellular hair in *Cannabis* are long and hooked whereas in *Humulus* they are short, hooked and contain a *cystolith*. In *Urtica dioca* (Fig. 8.10, B) the unicellular hair are called stinging hair. In *Verbena stricta* (Fig. 8.11) the leaf bears unicellular hair that are thick and pointed.

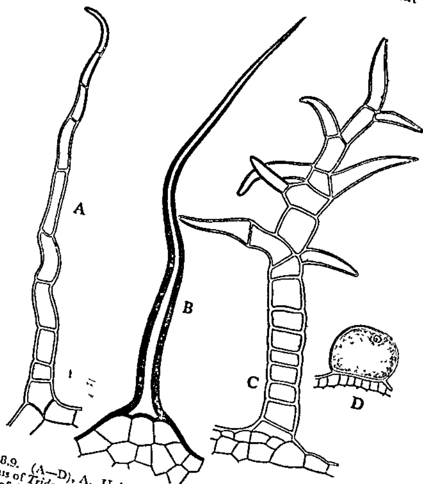


Fig. 8.9. (A—D), A, Uniseriate and multicellular hair from epidermis of *Tridax procumbens* (compositae). B, Unicellular hair from the stem of *Gossypium arboreum*. C, Dendroid hair from stem epidermis of *Withania somnifera*. D, Unicellular water vesicle from the leaf epidermis of *Mesembryanthemum crystallinum*

(b) *Multicellular hair*. These can be further classified as *uniseriate*

and *multiseriate*. Biseriate hair occur on the stem of *Lantana indica* (Fig. 8.9, H). Multiseriate hair occur on the leaf petioles of *Portulaca oleracea* (Fig. 8.10, B).

The uniseriate multicellular hair can be peltate (*Humulus*), branched, unbranched and stellate. The uniseriate unbranched hair are of various types In *Leucas asper* (Labiatae) the hair are two-celled (Fig. 8.10, F). Two-celled hair also occur on the stem of *Lantana* (Fig. 8.9, F). On the stem of *Clerodendron* (Fig. 8.10, G) the two-celled hair are small in size.

Many celled and unbranched uniseriate hair occur on the stems and leaves of many plants (Fig. 8.9, A) *e.g., Tridax procumbens.*

Branched uniseriate hair are known from many plants *e.g.* from the leaf epidermis of various species of *Cestrum* (Fig. 8.10, E.H). Branched uniseriate hair on the stem of *Withania somnifera* (Fig. 8.9 , C ; 8.10, D) give a tree-like appearance and are known as **dendroid hair** On the stem of *Sida, Gossypium herbaceum* (Fig. 8.9, E) and on the petioles of *Solanum melongena* (Fig. 8.10, C), the multicellular hair are **stellate.**

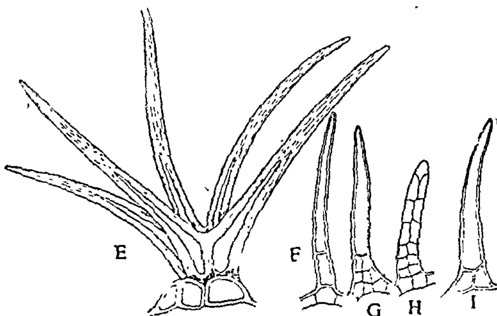


Fig. 8.9. (E—I). E, Stellate hair from the stem of *Gossypium herbaceum*. F, Two-celled hair from the stem of *Lantana indica*. G, Hair with multicellular base from the stem of *L. indica*. H, Biseriate hair from stem epidermis of *L. indica*. I, Hair with two celled base from the stem of *Lantana indica*.

The multicellular hair may have a two-celled (Fig. 8.9, F) or many celled base (Fig. 8.9, G) *e.g.* stem of *Lantana indica.*

In *Chenopodium album* (Fig. 8.10, A) the uniseriate hair possess a vesicle at the top and are known as **vesicular hair.**

The multicellular hair can be distinguished into two regions : (*a*) **foot** which is embedded portion of the hair and may be within the epidermal surface from whose cells it can be easily differentiated, and (*b*) **the body** which is above the epidermal surface.

The unicellular hair develop in two ways : (1) by prolongation of the outer wall of the epidermal cell and its growth in size : (2) the mother epidermal cell elongates and divides into a lower cell which functions as the epidermal cell and the upper cell which grows into a unicellular hair. In multicellular hair the outer cell may undergo further divisions and give rise to a multicellular structure. The cell walls of these unicellular and multicellular hair are made up of cellulose and are usually covered with a cuticle. Lignified walls and walls impregnated with silica and calcium carbonate are not rare. Cotton fibres that cover the testa of seeds are actually epidermal hair that become very long and have developed secondary thickenings of cellulose on their walls.

(*ii*) **Scales.** These are modified trichomes that consist of a discoid plate of cells mounted on a short stalk *i.e.*, the peltate trichomes can be designated as scales *e.g.*, *Olea* (Fig. 8.10 Q), *Humulus*.

(*iii*) **Colleters.** This term is derived from the Greek word *Colla* meaning glue. It includes all those unicellular and multicellular hair and peltate hair that are glandular in nature. They are found on many foliar organs *e.g.*, on bud scales, stipules, and on foliage leaves (*Nicotiana*, *Citrus*, *Boerhaavia* (Fig. 8.10), *Urtica*, *Aesculus*, *Rhododendron*, *Carya*, *Humulus*, *Ligustrum*). The epicarp of the fruit of orange bears numerous small and multicellular oil glands. In *Nerium oleander*, the epidermis of the leaf bears numerous multicellular trichomes that have a palisade-like secreting layer. In *Nicotiana tabaccum* the glandular trichome (Fig. 8.10,N) consists of a distincts foot embedded in the epidermis, a stalk, and a terminal glandular and a multicellular head. The stem of *Lantana indica* bears glandular hair with unicellular head (Fig. 8.10, M) or with two-celled head (Fig. 8.12, E). In *Leucas asper* (Fig. 8.10, K, L) the stem bears glandular hair with two-celled and many celled heads. In *Boerhaavia diffusa* (8.10, I) the stem epidermis bears glandular hair with many celled stalk and a one-celled head. In *Lantana indica* the glandular trichome develops from a mother cell (Fig. 8.12, A) which becomes distinct from the neighbouring epidermal cells. It enlarges (Fig. 8.12, B) and protrudes above the surface of the epidermis. A transverse wall (Fig. 8.12, C) appears. The lower cell functions as foot and the upper cell divides again into two cells (Fig. 8.12, D), the upper developing into a two-celled head (Fig. 8.12, E) and the lower into a single-celled stalk.

(*iv*) **Water Vesicles or Bladders.** These are bladder-like or vesicular trichomes that are greatly swollen or distended epidermal cells, which probably store water (Fig. 8.9, D). These can be best demonstrated in *Mesembryanthemum crystallinum* (Ice plant) by cutting a transverse section through the petiole of the leaf. The vesicles in this case are unicellular and contain a thin cytoplasmic layer that encloses a big central vacuole.

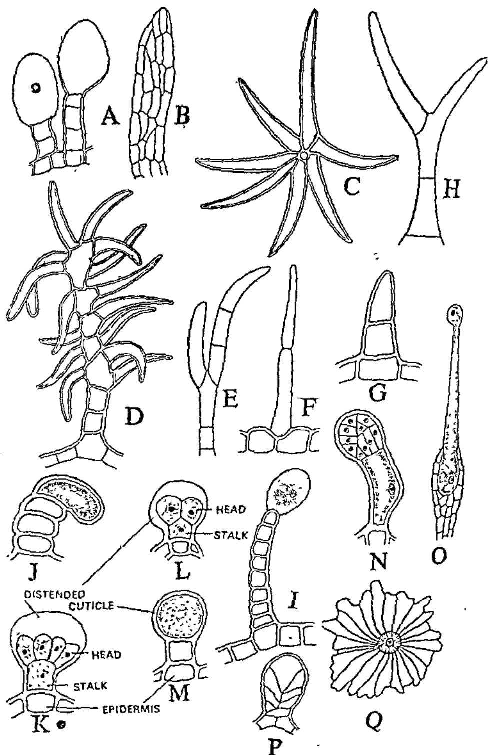
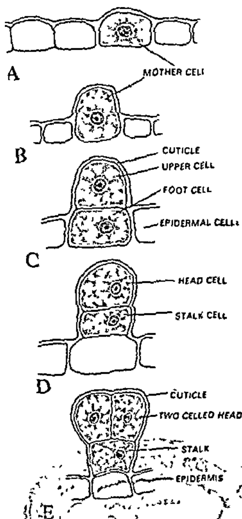


Fig. 8.10. (A—Q). Hairs. A, Vesicular hair from the leaf of *Chenopodium album*. B, Multiseriate or spongy hair from the petiole of *Portulaca oleracea* (*Continued*)



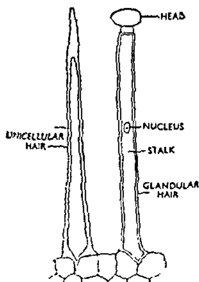


Fig. 8.11. Hairs from the leaf of *Verbena stricta*, one of them is unicellular and pointed and protective. The other is thin-walled and capitate and multicellular.

Fig 8.12. (A—E) Various stages in the development of glandular trichome in *Lantana indica*.

C, Stellate hair ... D, Dendroid hair from the stem o ... of *Cestrum purpuresc* ... the ... *dron* ... *tum* I, ... rom the ... *Leucas* ... ar hair ... is not ... *im.* O, ... Short ... *iberosum* ... It has a short stalk.

Taxonomic and Phylogenetic Importance of Trichomes. Trichomes have been regarded by some authors (Sporne, 1956 ; King and Robinson, 1969, 1970 ; Ramayya, 1972) to be of significance in determining taxonomic status and phylogenetic relationship of angiosperms. King and Robinson (1969, 1970) used trichome types and some epidermal features in determining generic limits among the *Compositae*. Ramayya (1972) gives a significant data of trichome types among **Magnoliales**, that helps us to distinguish the various families of this order. The family *Magnoliaceae* has unicellular hairs and uniseriate hairs. These are absent in *Illiciaceae*, *Winteraceae*, *Canallaceae*, *Schizandraceae*, *Lactoridaceae* and ... *Himantandraceae* has ... nargins peltate scales and stellate hairs. ... o other have peculiar glandular emergenc ... orders will prove to be of great use.

B. **Root Hair.** The root hair arise just behind the zone of active cell division. They are always unicellular and unbranched and are direct lateral extensions of the epidermal cells of the root. Their walls are generally thin and made up of cellulose with an outer covering of ... forms a thin lining layer with the ... There is single large central vacu- ... and mineral substances. The root hair cannot live long and die after a few days or a few weeks. In some members of *Compositae* the root hair persist for one growing season and have thick and lignified walls. The new root hair develop near the tip, as the root grows, and the old ones collapse. The new root hair do not arise among the older ones.

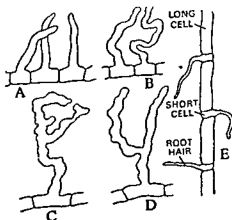


Fig 8.13. (A—E). Root hair, A Root hair From plants growing in water ; B from plants growing in moist soil ; C—D, From plants growing in dry soil ; E. Part of root epidermis of *Angiozanthos* showing small, short cells (trichoblasts) and long cells. Short cells give rise to root hair.

Cormack (1949) studied the development of root hair and reported that the epidermal cells which give rise to root hair have slow vertical growth because the walls of plastic pectic acid on the walls of these cells gets transformed into a harder calcium pectate. In *Cyperus* and *Angiozanthos* the root epidermis exhibits two types of cells: (1) root hair forming cells that are smaller in size ; (2) longer cells than cannot produce root hair (Fig. 8.14, E). Leavitt (1904) reported that the smaller root hair forming cells show denser cytoplasmic contents than the longer cells. The term **trichoblas**[t] has been used for these smaller root hair forming cells. Fig. 8.1[3] A—D shows the variations in root hair from plants growing in water, moist soil and dry soil.

Functions of Epidermis Tissue System. This system performs a variety of functions which can be listed as below :—

(1) To reduce the rate of transpiration due to the cuticularisation of the outer walls of the cells of this layer.

(2) It protects the underlying tissues.

(3) It helps in gaseous exchange due to the presence of stomata.

(4) Storage of water and metabolic products The water vesicles and bladders in the epidermal cells of ice plant serve this function.

(5) The root hair in root epidermis serve the function of absorption of water and also increase the surface area of absorption of the root.

(6) In some cases the epidermal cells contain choloroplasts and help in photosynthesis. It is also said to supply water to the underlying photosynthetic tissue.

(7) Various glandular trichomes secrete various products.

(8) This layer has also meristematic potentialities and resumes active cell division during the formation of **phellogen** and in the healing of wounds.

FASCICULAR SYSTEM OR VASCULAR SYSTEM

This system is made up of varying number of strands or bundles, called the vascular bundles, that are embedded in a central cylinder of the shoot or the root. It is also called the **stele** and is surrounded by the cortex and epidermis. The stele is composed of **pericycle, vascular bundles, pith** and the **medullary rays.** Its chief function is conduction of wate strength. The dicots, there is the xylem Th absent in mor and the phlc but form sepa nts of the vasc primary mer liffers in diffe hey are arranged in the form of a ring in the dicot stems (exceptions are there) and are often red in the monocot stems. While plant one is struck by its continuity.

In *Eupatorium ayapana* (*Compositae*) there is no endodermis and pericycle in the young and old stem (G.C. Mitra, 1972). Moreover, the pith in this case also originated from the s of the procambial strands tissue. Absence of pe others falsifies the ste which regards pericycle (or by some endodermis) as the outermost boundary of the stele. Such examples have led many

anatomists to use the term **vascular region** instead of **stele** (Esau, 1943, 1948).

Leaf Traces and Leaf Gaps. A shoot is distinguished into nodes and internodes. Leaves arise at each node. A portion of the vascular cylinder, at each node, is deflected into the leaf, where it differentiates itself into a vascular system characteristic of the leaf. If we trace back the vascular bundles of the leaf into the stem, it is seen to be individually distinct upto varying depths in the tissues of the stem but ultimately it merges into the vascular system of the stem. Part of the vascular strand of the leaf which is present in the stem as a lower portion of the vascular supply to the leaf is called the **leaf trace.** In other words, a leaf trace (Figs. 8.14 & 8.15) is a part of the vascular cylinder that extends between the leaf-base and the point where it merges with the vascular system of the stem. The number of leaf traces associated with one leaf may be more than one.

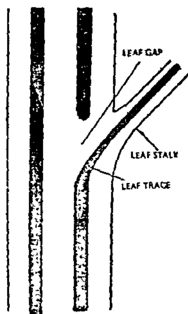


Fig. 8.14. L.S. stem showing leaf-trace and leaf gap. (Diagrammatic).

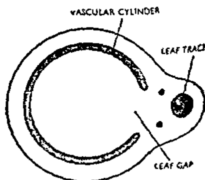


Fig. 8.15. T.S. stem showing leaf trace and leaf gap (Diagrammatic).

In seed [illegible] the portion, lying immediately above [illegible] from the vascular cylinder of [illegible] the parenchymatous region the [illegible] n is limited to only a short distance up, [illegible] ue is present. These parenchymatous region [illegible] vascula [illegible] re described as **leaf gaps** (Figs. 8.14 and [illegible] na [illegible] ot actually [illegible] the continuity [illegible] cyl [illegible] e vascu-

The leaf gaps can be clearly recognised in those ferns and angiosperms where the vascular system forms a more or less continuous vascular cylinder in the internodal regions. In some cases, the leaves are so crowded that the gaps at successive nodes overlap each other and the vascular cylinder appears to be dissected. In a cross-section such a vascular cylinder is seen to be composed of a circle of vascular bundles with intervening parenchymatous areas (leaf-gaps). In most of the angiosperms the vascular system is composed of anastomosing strands. In such cases the leaf gaps become confluent with the parenchymatous tissues between the two vascular bundles (*interfascicular areas*) and it is difficult to distinguish *between the leaf gap and the interfascicular area.*

In the monocots there are numerous leaf traces to a single leaf and these have been distinguished into two types : (*i*) Small and (*ii*) Large. The former extend only upto the peripheral region of the stem, whereas the latter reach the centre of the stem, bend downwards and then reorientate towards the periphery where they unite with the peripheral bundles.

Th[illegible] leaf trace to a leaf are [illegible] des with three leaf-gaps [illegible] **trilacunar** (Fig. 8.16, C). In case there are several leaf-gaps to a single leaf at a nodes the node is called **multilacunar.** Sometimes, the unilacunar nodes give out more leaf traces than one (Fig. 8.16, B).

Fig. 8.16. (A—C). A, Unilacunar node with one leaf trace. B, Unilacunar node with three leaf traces. C, Trilacunar node with three leaf traces. (*After Fahn*)

Branch T[illegible] G [illegible] cular [illegible] vas- [illegible] that [illegible] nch [illegible] just [illegible] the [illegible] a sing [illegible] is [illegible] erse

section of the node will show the vascular system of the main stem, then the branch gap, branch-trace, then the leaf-gap and finally the leaf-trace (Fig. 8.17 and 8.18).

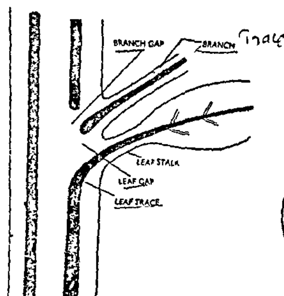


Fig. 8.17. Diagrammatic L.S. through a node showing leaf trace, leaf gap and branch gap and branch trace.

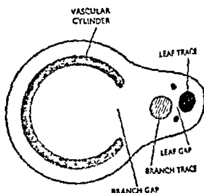


Fig. 8.18. T.S. through a node (diagrammatic) showing branch trace, branch gap and leaf gap and leaf trace.

Types of Vascular Bundles. A vascular bundle when fully formed is generally composed of two well-defined complex tissues called

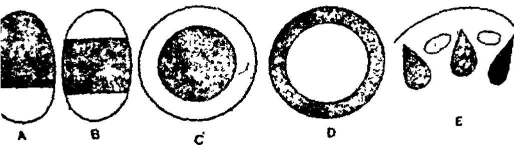


Fig. 8.19 (A—E) Showing types of vascular bundles. A, Collateral, B, Bicollateral, C, Amphicribral, D, Leptocentric or amphivasal. E, Radial; Black colour denotes xylem, uncoloured and stippled areas represent phloem.

the xylem and the phloem. The vascular bundle is said to be **conjoint**, if it consists of both xylem and phloem. It is said to be **open** if cambium is present. In most c ... the outside of the xylem strand an ... **collateral** (Fig. 8.19, A). In case phloem ... the bundle is said to be **bicollateral** ... seca

the cambium is absent the vascular bundle is said to be **closed**, as in monocots and vascular cryptogams.

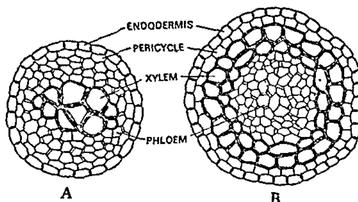


Fig. 8.20. (A—B) Concentric Bundles

A ; Amphicribral vascular bundle from *Polypodium* rhizome.
B ; Amphivasal vascular bundle from stem of *Cordyline*.

In case one tissue completely surrounds the other the vascular bundle is called **concentric** (Fig. 8.19 C—D) ... bundles are of two types : (i) a... **amphicribral** (*Polypodium*) concen... surrounds the xylem (Figs 8.19, C ; ... bundles the xylem completely su... 8.20 B) as in *Acorus, Cordyline, Conv... majus*.

In roots there are separate strands of phloem and xylem that are separated by parenchymatous cells and show a radial arrangement (Fig. 8.,19 E). Such vascular bundles are said to be **radial**.

In the collateral vascular bundles the phloem starts differentiating from the margins adjacent to the peripheral part of the stem and proceeds towards the centre of the bundle. The differentiation of the xylem begins from an opposite point and proceeds towards the centre. As a result, the first formed xylem elements or the **protoxylem** is next to the pith and the first formed phloem elements or the **protophloem** is formed next to the pericycle.

In ... ied in the formation of t... closed collateral bundle. If some meristem rem...

STELAR SYSTEM

The primary vascular system in the plants has been interpretted in different ways by a number of workers. De Bary (1884) considered the individual vascular bundle to be the basic unit of primary vasculature of a plant. He believed that a single meristele of *Dryopteris* was morphologically equivalent to the entire protostelic cylinder of *Selaginella* or of *Gleichenia*. The unity of the vascular system was subsequently

recognised, however, and emphasized by Van Tieghem and Douliot (1886) in their formulation of the stelar theory. Under this concept all meristeles in the rhizome of the *Dryopteris*, collectively, would be considered morphologically equivalent to the single protostelic cylinder of *Gleichenia* or *Selaginella*. The term **stele** (Greek word meaning column) is applicable only to the primary vasculature of the shoot. Van Tieghem and Douliot *regarded the stele to be the core of the axis which includes the vascular system, the interfascicular portion, the pith and some surrounding portions of the fundamental tissue in the vicinity of the vascular bundles* (pericycle, endodermis). This concept of the stele was widely accepted by the plant morphologists and plant anatomists. This stelar concept subsequently [illegible] elaborations through the works of [illegible] Vaughan 190[illegible] stele in 1930) It is ve[illegible] the case of most of the seed plants, as there is no clear cut demarcation between the cortex and the stele. Absence of a well defined endodermis and a pericycle in the stems of many seed plants has led the modern anatomists to discard the term stele in its original sense and replace it by the term **vascular cylinder**. In the lower plants where there is a clear demarcation between the central vascular cylinder and the cortex, the term stele can be used in the real sense of its definition.

Types of steles (Fig. 8.22). Jeffrey (1899, 1902) recognised two basic types of stele ; (*i*) **protostele** and (*ii*) **the siphonostele**. He derived the latter from the former by the appearance of pith in the centre. Appearance of leaf gaps in the siphonostele led to the appearance of a much dissected stele called the **dictyostele**. He further concluded that the vascular cylinder of the seed plants, namely the **eustele** (Brebner, 1902) was derived from the filicalean dictyostele by further reduction of the vascular tissues.

1. Protostele. It is the primitive and the simplest type of stele (Fig. 8.21). In this case there is no pith in the centre. The centre is occupied by xylem which is surrounded by phloem pericycle and endodermis. In its simplest form the central core of xylem is surrounded by a uniform layer of phloem. Brebner (1902) [illegible]ed the protostele into two types : (*i*) *haplostele* and (*ii*) *actinost*[illegible] [illegible] is surrounded by a uniform layer of ph[illegible] *S. chrysorhizos*. *S. kraussiana*. *S. flabellata*.

in *Selaginella selaginoides*, the central core of xylem becomes star-shaped or forms varying number radiating ribs The protoxylem is at the tip

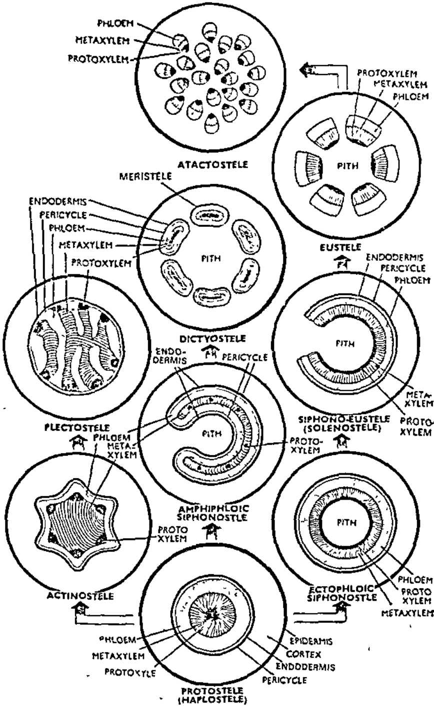


Fig. 8.21. Various types of steles.

of each rib. The phloem occurs in patches in the concavities or sinuses of the star-shaped xylem. It does not form a uniform layer (Fig. 8.21). Such a protostele is called **actinostele.** In case the radiating ribs of xylem deepen to an extent that they appear as separate parallel lobes with phloem lobes alternating with them then the protosele is termed as **plectostele** (Zimmermann, 1930) *e.g., Lycopodium volubile* (Fig. 8.21). In *Gleichenia dichotoma* and *L. cernuum* the protostele consists of irregular groups of xylem tracheids mixed with phloem or with parenchymatous cells. Such a condition is designated as **mixed protostele.** Among the angiosperms this condition is found in the stem of *Limnanthemum* (Fig. 17 13). The stems of *Hydrilla* (Fig. 17.9). *Potamogeton pectinatus* (Fig. 17.11), *Elodea* (Fig. 5.7), *Myriophyllum* (Fig. 17.1) are other angiosperms that show a protostelic organisation.

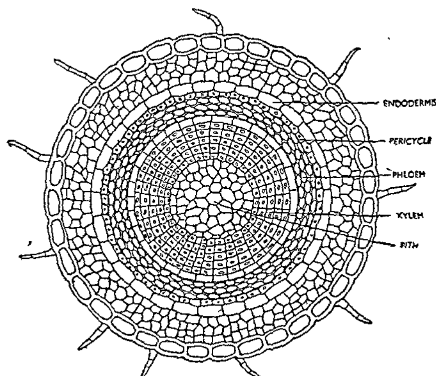


Fig. 8.22. T.S. stem of *Phlox* showing ectophloic siphonostele (Diagrammatic).

2. Siphonostele. The appearance of pith in the centre of the protostele changes it into a siphonostele (Fig. 8.21). The first step in thir direction is illustrated by ferns like *Gliechenia dichotoma* in which scattered groups of parenchyma make their appearance among the xylem tracheids. Later developments lead to the appearance of a definite parenchlymatous core surrounded by xylem, phloem, pericycle and endodermis. The parenchymatous core is the pith or the medulla and such a medullated protostele is called the siphonostele. Among the

angiosperms this condition is nicely portrayed by the stem of *Hippuris* (Fig. 17.8).

The siphonostele is further classified into : (*i*) **ectophloic siphonostele** and (*ii*) **amphiphloic siphonostele** or **solenostele.** In ectophloic siphonostele pericycle and endodermis are found only external to the phloem *e.g.*, in ferns like *Osmunda* and in angiosperms like *Phlox* (Fig. 8.22), *Lindenbergia, Nicotiana* and *Salix*. In the **amphiphloic siphonostele** endodermis and pericycle are present next to phloem as well as next to pith *i.e.* there is external as well as internal enodermis *e.g., Marsilea, Adiantum* etc. In the angiosperms such a condition exists in some members of *Asclepiadaceae, Convolvulaceae* and *Solanaceae.* This condition is regarded as primitive of the two types. In case the

gap it is called **phyllosi-** angiosperms and *Adiantum* perforated by a leaf gap, itis

There are two views regarding the appearance of pith in the protostele. These are : (*i*) intrastelar origin of pith ; and (*ii*) extrastelar origin of pith. The proponents of intrastelar origin of pith (Boodle), 1901 ; Gwynne-Vaughan, 1918 ; Bower, 1911; Petry, 1914 ; Thompson 1920 ; Fahn, 1960) believed that the pith arose by the metamorphosis of inner vascular tissue into parenchyma. Such a view is now held to be true as a result of observations on many ferns and in an angiosperm, *Hippuris* (see chapter 11). The second view was put forth by Jeffrey (1902, 1917) who believed that pith appeared as a result of invasion of the parenchymatous cells of the cortex into the stele. This he believed took place through the leaf gaps and branch gaps.

Another modification of the siphonostele is called the **dictyostele** (Fig 8.21). It is found in some ferns *e.g., Dryopteris, Pteris, Pteridium,* etc. In this case the siphonostele gets dissected by several overlapping leaf-gaps with the result that the stele appears dissected into a network-like structure. The meshes of the network are the parenchymatous leaf-gaps. The network is made up of longitudinal strands. Each strand is called a **meristele.** In a transverse section (Fig. 8.21) the meristeles are arranged in a ring and each meristele is separated from its neighbour by a leaf gap on either side. Each meristele is comparable to an amphicribral, concentric vascular bundle with a central xylem ... endodermis ... loem, pericycle and *laceae* and *Ac* ... members of *Primu-* ... *nthaceae*, Fig. 8.23) the dictyostelic stem possesses a ring of outer meristeles surrounding a single central meristele.

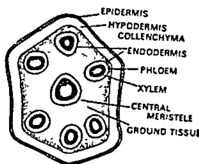


Fig. 8.23. *Dirnthera americana* ; Outline sketch of T.S. stem.

Wardlaw (1952) experimented on *Dryopteris* and demonstrated that stelar structure in this fern can be changed from a *dictyostele* to *siphonostele* with a continuous cylinder by removing the leaf primordia.

In *Pteridium aquilinum* and *Matonia pectinata* the stelar system consists of two or three concentric rings of *meristeles. Such a stele is* called **polycyclic dictyostele.**

In the seed plants the vascular cylinder is dissected by both the [illegible] widely scattered network of vascular bundles. Such a stele is called **atactostele** (Fig. 8.21).

A different interpretation of vascular cylinder of seed plants is that it consists of a number of discrete vascular bundle sympodia. Nageli (1858) illustrated the vascular systems of several dicotyledons as cylinders of sympodia. Geyler's studies on gymnosperms (1867) yielded similar results that have been recently corroborated by Scott (1923), Namboodiri and Beck, (1968), Beck, (1970), and in angiosperms by Devadas and Beck (1972). De Bary (1884) wrote that the vascular bundles in angiosperms are connected in a unilateral sympodial manner, or in a reticulate manner. Balfour and Philipson (1962), *Esau (1965) and Benzing (1967) have also described the primary* vascular system of some dicotyledons in terms of sympodial systems. The leaf-gaps are not easily definable in seed plants because these are confluent with the medullary rays. It is questionable whether the leaf gaps of seed plants are morphologically equivalent to those of ferns. Jeffrey equated them with ferns and proposed that eustele originted from the ectophloic siphonostele *by the appearance of such leaf gaps.* Recent interpretations of the eustele in gymnosperms by Namboodiri and Beck (1968 *a, b, c*) and Beck (1970) militate against the presence of either a filicalean type of siphonstele or filicalean leaf gaps in gymnosperms These authors present evidence which they interpret as showing that the eustele in progymnosperms and in Lyginopterid gymnosperms *evolved directly from the protostele through longitudinal* dissection without any intervening siphonostelic stage. If we believe that angiosperms originated from a group of pteridospermous gymnosperms, then it follows that there may be no leaf gaps of the fern type in angiosperms as well (Devadas and Beck, 1972). This view has also been expressed by Sporne (1958) and Birenda Slade (1971).

Devadas and Beck (1972) *state,* "If we accept, therefore, the suggestion that the sympodia of angiosperms, like those of *Lyginopteris,* may have evolved from a protostele by way of some similar pteridosperms, one must conclude that the continuing bundles of the sympodia from which leaf traces diverge are cauline. The protostele is clearly an axial, not a foliar structure. That this is true becomes very apparent when one considers that the ancestral psilophytes, from which the protostelic progymnosperms must have evolved, were leafless. It is for these reasons, therefore, that we refer to the main bundle of the sympodium as an axial bundle and consider that leaf traces are bran-

The pericycle in some cases *e.g.*, Sun-flower has been proved to originate from the protophloem elements and forms a part of the vascular bundle. In most of the monocot stems, the ground tissue system is composed only of the parenchymatous cells in which are embedded varying numbers of vascular bundles. In such cases distinction into cortex, pericycle, endodermis, and pith is absent.

C... ...hat lies be... ...ermost la... ...yers in th... ...paren-chymatous and may be rounded or polygonal, cylindrical, and in some cases stellate. The cells have prominent inter-cellular spaces and in some cases the intercellular spaces are large and also known as air-spaces. Chloroplasts may be present in all cortical cells or at least in some of them. ... of various types are some of t... In *Helianthus* and ... immediately beneath the epidermis. In the former case the collenchyma is in the form of a cylinder, whereas in *Cucurbita* it is restricted to the ridges of the stem and forms strands. In some cases the cortex has a layer or more of sclerenchymatous cells that are classified as cortical fibres. In the cortex of *Trochodendron* stem, there are present much branched sclereids called **astrosclereids**. Resin ducts, oil ducts, laticiferous cells, laticiferous ducts are other structures that are found in the cortical cells of various plants.

The functions of the cortex include protection, storage, photosynthesis etc. In the roots the cortex helps in pumping the water, absorbed by root-hair, into the xylem vessels.

Endoderms. It is a single layer of compactly arranged cells which are generally parenchymatous, but have distinctive wall characteristics. The cells constituting this layer are elongated with their long axis parallel to the vascular tissue. In transverse section the cells appear barrel-shaped, oval or elliptical. The cells are generally living and ... crystals are ... wall material ... material is ... is **casparian** strip ... band ... nin reactions ... section these ... **casparian dots.** ... casparian strip ...

than the aerial stems. In *Senicio* and *Leonurus* the endodermis is reported to develop only when the plants reach the flowering stage (Warden 1935; Datta 1945).

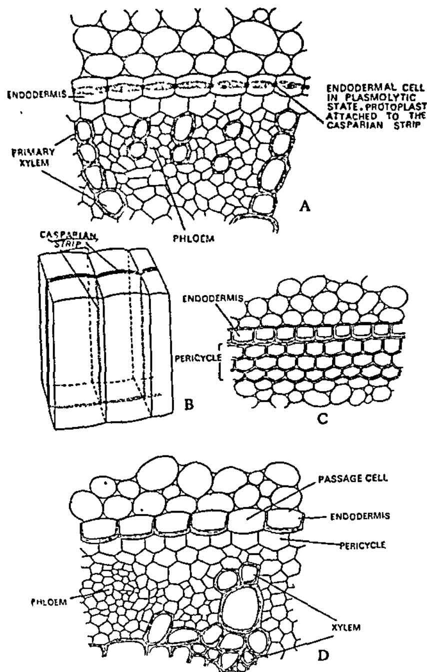


Fig. 8,24. (A—D). Ground tissue system. A—B, Endodermis from the root of *Convolvulus arvensis*. C, Endodermis from the root of *Smilax* with all the walls thickened, pricycle is also sclerenchymatous. D, Endodermis from the root of Maize showing radial and innerwalls thick.

In the roots tne cells of endodermis devolop thick walls. Usually, the radial and the inner tangential walls are thick and the outer walls

The pericycle in some cases *e.g.*, Sun-flower has been proved to originate from the protophloem elements and forms a part of the vascular bundle. In most of the monocot stems, the ground tissue system is composed only of the parenchymatous cells in which are embedded varying numbers of vascular bundles. In such cases distinction into cortex, pericycle, endodermis, and pith is absent.

Cortex. The cortex when clearly delimited is the zone that lies between the endodermis (if it is not considered to be the innermost layer of cortex) and the epidermis. It may be few to many layers in thickness. The cells in most of the cases are thin-walled and parenchymatous and may be rounded or polygonal, cylindrical, and in some cases stellate. The cells have prominent inter-cellular spaces and in some cases the intercellular spaces are large and also known as air-spaces. Chloroplasts may be present in all cortical cells or at least in some of them. ... of various types are some of ... In *Helianthus* and ... immediately beneath the epidermis. In the former case the collenchyma is in the form of a cylinder, whereas in *Cucurbita* it is restricted to the ridges of the stem and forms strands. In some cases the cortex has a layer or more of sclerenchymatous cells that are classified as cortical fibres. In the cortex of *Trochodendron* stem, there are present much branched selereids called **astrosclereids**. Resin ducts, oil ducts, laticiferous cells, laticiferous ducts are other structures that are found in the cortical cells of various plants.

The ... photosynthesis et ... absorbed by ...

Endoderms. It is a single layer of compactly arranged cells which are generally parenchymatous, but have distinctive wall characteristics. The cells constituting this layer are elongated with their long axis parallel to the vascular tissue. In transverse section the cells appear ... living and ... are ... erial ... al is ... rian ... strip band ... tions ... hese ... dots. ... casparian strip ... n of ... ts of ... it is present in all the pteridophytes, ... angiosperms. Guttenbreg (1914) is ... possess a more distinct endodermis than the aerial stems. In *Senicio* and *Leonurus* the endodermis is reported to develop only when the plants reach the flowering stage (Warden 1935; Datta 1945).

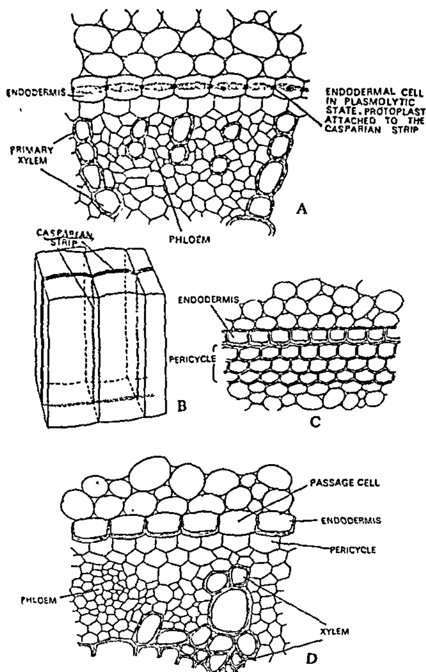


Fig. 8,24. (A—D). Ground tissue system. A—B, Endodermis from the root of [illegible] ... [illegible] it of *Smilax* with all the [illegible] D, Endodermis from the [illegible]

In the roots the cells of endodermis devolop thick walls. Usually, the radial and the inner tangential walls are thick and the outer walls

remain thin (Fig. 8.24) *e.g.*, roots of maize. In some roots [illegible] *Smilax rotundifolia* (Fig. 8.24) all the walls are thickened. The thickening is due to the laying down of suberin material over the eariler formed walls and the casparia n strips In *Smilax rotundifolia* the thickening is sometimes developed to an extent that it nearly closes the lumen. The thickening material in the later stages may be of cellulose [illegible] at certain places by the [illegible] cells or the transfusion [illegible] of suberin and, in [illegible] cells, ar[illegible] ro[illegible] The [illegible] in[illegible] It is [illegible] w[illegible]
termed as **secondary endodermis** or **phloeotrema**.

In the pteridophytes and the dicotyledonous angiosperms the endodermis is thin-walled and is often called the **primary endodermis**.

Several functions have been ascribed to this layer. These can be listed as below :—

1. It acts as a water-tight dam between the vascular and the non-vascular regions because the cells are compactly arranged and have no intercellular spaces.

2. It can be regarded as an air-dam between the vascular and non-vascular regions preventing the entry of air into the conducting elements and thus saving them from clogging.

3. In some cases it stores starch in its cells and may act as storage layer.

4. The presence of passage cells in the root endodermis suggests that it serves as a passage of water from the cortex to the xylem.

5. It may serve as a protective layer in the root of monocots, especially when the cortex has sloughed away.

6. It maintains root pressure.

7. In some cases the thin-walled endodermis (primary type) may become meristematic and form **cork cambium**. It occurs frequently in the roots and occasionally in the stem.

phloem group of the vascular bundles. It has now been shown that these thick-walled fibrous layers of pericycle are a part of primary phloem. Same is the case in *Linum* (flax) and *Cannabis* (hemp). The sieve elements of the protophloem become obliterated and the other cells of the **protophloem** differentiate into fibres So in such cases the tissue between the endodermis or cortex (if endodermis is absent) and the vascular system is not actually pericycle but a part of the phloem. The term **perivascular fibres** is used in such cases to designate these thick-walled cells.

The pericycle, when composed of parenchymatous cells may act as a storage region. In the dicot roots the cells of the pericycle become

of vascular cambium. Thick-

to the plant. In some cases

nals, laticiferous cells, etc.

Pith. It occupies the centre of the stem and the root and occurs in the form of a column of tissue. It is generally composed of large parenchymatous ... of intercellular spaces, but sclerenchym-

laticiferous tubes, and medullary vas-

in the pith. Ontogenetically, the pith

develops from ...

rapid elongation and radial expansion of the stem. In such cases the pith is represented by a hollow cavity. In its earlier stages of development the pith has smaller cells with living contents and even chloroplasts, but as it matures the cells may become dead and lose all contents or the pith contains various proportions of living and dead cells. The living cells in the pith generally store starch and other fatty substances.

The peripheral portion of the pith is in some cases easily distinguishable from the central portion or the medulla, by the smaller size of its cells, their living contents, and sometimes by the presence of chloroplasts in the cells (*Lantana*, *Anagalis* etc.). The zone is called the **perimedullary zone** of pith.

In most of

layers of the

with the pe

densely pack

pith between ... pith rays medull-

ary rays.

In such cases

the central pith. In some members of the families *i.e.*, *Umbelliferae* and *Compositae*, the pith rays are composed of sclerenchymatous cells or of both sclerenchymatous and parenchymatous cells.

The main function of the pith is to store food materials. In case it is sclerenchymatous ... plant. The

as c

to t

rays become meristematic and give rise to interfascicular cambium,

up of two types of cells : (1) the **fusiform initials,** and (2) the **vascular ray initials.** The fusiform initials, when seen in a tangential longitudinal section are elongated prosenchymatous cells (Fig. 9.1, A. I and II) which sometimes may achieve a length of 5,000 μ (Bailey, 1920, 1923, 1930). These cells form the **axial system** of secondary vascular tissue *e.g.*, sieve cells, companion cells, phloem parenchyma, phloem fibres, vessels, tracheids, xylem fibres and xylem parenchyma. The vascular ray initials of the cambium are small isodiametric cells which, by their division, give rise to the **radial systems** of the vascular tissue *e.g.*, the phloem and the xylem rays. In a tangential section the fusiform initials of the cambium show two types of arrangements in different plants. In one type, fusiform cells are arranged in horizontal rows with the ends of the cells at the same level (Fig. 9.3, A). Such an arrangement is called **storied** or **stratified arrangement and the cambium** is called **stratified** or **storied cambium.** In case the fusiform cells show no regular arrangement and their ends overlap, the cambium is called **non-storied** or **non-stratified cambium** (Fig. 9.3, B). The former type of cambium gives rise to **storied wood** whereas the latter type gives rise to **non-storied wood.**

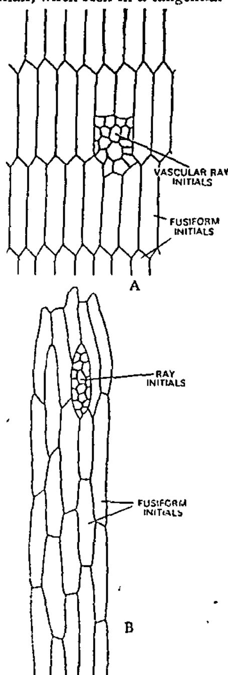


Fig. 9.3. A, Storied cambium in a tangential section.
B. Non-storied cambium in a tangential section.

The cells of the cambium divide periclinally (Fig. 9.4) and cut off derivatives either towards inside (towards [illegible] towards [illegible] loem). [illegible] wards [illegible] into [illegible] those produced [illegible] w[illegible] el[illegible] derivatives are exactly like the cambial cells (Fig. 9.4, A—D) and possess primary walls. It is difficult to distinguish between the derivative cells and the cambial cells. The

cambium, therefore, appears to be many-layered. It is actually one-layered and the xylem and the phloem derivatives along with the

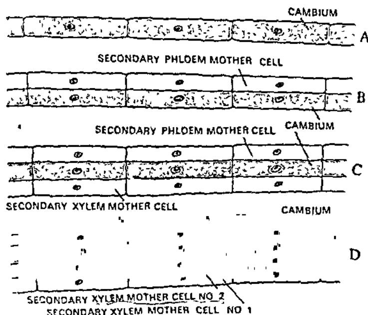


Fig. 9.4. It illustrates division of the cambium cells to cut off xylem and phloem elements.

cambium are designated as **'cambial zone'**. The activity of the cambial cells produces radial files of xylem derivatives towards the inner side and the phloem derivatives towards the outer side. Both the files meet at the cambial initial. The xylem and phloem derivatives undergo one or more periclinal divisions before maturing into xylem and phloem cells. Bannan (1955, 1957) regards these cells as **xylem mother cells** and **phloem mother cells.**

Fascicular and Interfascicular Cambium. The fascicular cambium is the strip of uniseriate cells that separates the **metaphloem** from the **metaxylem** in the vascular bundles of the gymnosperms and the dicots. It is derived from the procambial cells that do not transform into primary phloem and primary xylem elements. The fascicular cambium is absent in the monocots, because in these the metaxylem and metaphloem elements meet in the centre and the growth of the vascular bundle stops (it is known that the primary phloem and the primary xylem elements start differentiating from the outer and the inner edges of the procambial strands respectively.)

In some dicots the fascicular cambium is restricted only to the original vascular bundle and the areas between the various vascular bundles (interfascicular area) develop into vertical strips of parenchyma. In of the woody and herbaceous dicot stems the interfascicular areas

also develop strips of cambial cells that become laterally joined with
ntinuous cylinder of
lop in the interfasci-
The time of appear-
eatly in different pla-
nts. In some plants the interfascicular cambium differentiates even before the maturation of the primary phloem and the xylem. In *Aristolochia* and *Clematis*, on the other hand, the interfascicular cambium develops very late and arises by the tangential division of the cells of the medullary rays between the two vascular bundles.

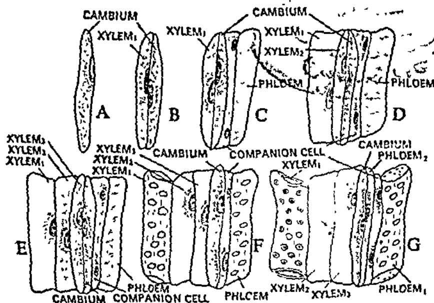


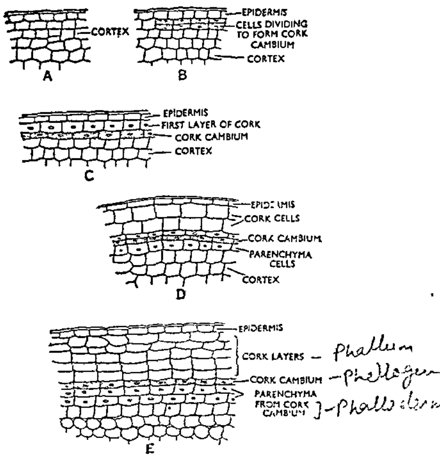
Fig. 9.5. It shows division of cambial cell to cut off secondary xylem and phloem elements.

The Cambium of Monocotyledons. The monocots as a class are regarded as destitute of cambial activity. This is true of the herbaceous monocots *e.g.*, grasses, where the vascular system is made up of a number of scattered vascular bundles. The bundles are generally **collateral**, but in some monocots *e.g.*, *Acorus* and *Cordyline* the bundles are **amphivasal.** In the *palms*, Ball (1941) has described the presence of a "primary thickening meristem", which by its activity adds to
cells in the ground tissue and
(1941) described a cambium-
ratified arrangement and is
homocellular.

In *Yucca, Dracaena, Cordyline, Nolina, Agave* and *Dasylirion* there is

the stem.

[illegible] the epidermis, hypodermis, cortex [illegible] e phloem ray cells). Its activity [illegible] ie root, because its cells divide in a tangential plane cutting off cells towards its inner as well as outer face. It is composed of a single layer of meristematic cells that do not show much variation in shape and size (Fig. 10.1, C). In a transverse section the cells appear almost rectangular and radially flattened. The cells have vacuolate protoplast that may contain chloroplasts and other cytoplasmic inclusions. Tannins are also present in these cells. The cell contents are granular and the cells are compactly arranged except in the lenticels.



[illegible] pment of periderm in *Prunus* [illegible] velops from cortical cells lying [illegible] k or phellem thus develops [illegible] cut off towards inner side and the cork layers increase in number.

The phellogen originates at different depths outside the vascular cylinder. In *Pyrus* and *Nerium* the epidermal cells become meristematic,

10

PERIDERM AND ABSCISSION

THE PERIDERM

The term **periderm** is ... protective secondary tissue that develops by the activity of ... nd replaces ... ure of the the epidermis which is rup ... uced in the increasing secondary vascular tissue. ... It develops in leaves and in most of the monocot stems and roots. It also develops in some majority of woody dicots and gymnosperms. It also develops in some herbaceous dicots. Some woody dicots *e.g.*, *Acer*, *Acacia*, *Eucalyptus*, ... etc. do not form periderm because in these cases the ... (cortex, epidermis) keep ... cell division ... in different and cell enlargement ... after the initiation of the secondary growth plants. It may develop soon after the initiation of the secondary growth or it may develop late. It depends upon the capacity of the cells of the primary tissues outside the secondary phloem to divide and enlarge. In case they cannot keep pace with the enlarging diameter of secondary vascular tissue, they undergo rupturing and tearing due to the increasing ... vascular cylinder and there is necessity of ... **periderm**. In case they can keep pace and can ... of periderm is delayed till they retain ... m (1953, pp. 285—294) reported ... the secondary xylem in some dicot the development of periderm ... the secondary xylem in some dicot families and termed it as **interxylary cork**. Periderm also develops when a stem or a root is wounded and is termed as **wound periderm**. It also develops at places where the stem and its branches are exposed as a result of leaf-fall. Its development is also recorded in relation to parasitic attack by bacteria and fungi.

STRUCTURE OF PERIDERM. The periderm is made up of three tissues : (*i*) **Phellogen** or the **cork cambium** ; (*ii*) the **phellum** or the **cork layers** ; and (*iii*) the **phelloderm** or the living parenchymatous tissue.

1. **The Phellogen**. It is a secondary lateral meristem that may arise

from the ... pidermis, hypodermis, cortex ... hloem ray cells). Its activity ... ot, because its cells divide in a tangential plane cutting off cells towards its inner as well as outer face. It is composed of a single layer of meristematic cells that do not show much variation in shape and size (Fig. 10.1, C). In a transverse section the cells appear almost rectangular and radially flattened. The cells have vacuolate protoplast that may contain chloroplasts and other cytoplasmic inclusions. Tannins are also present in these cells. The cell contents are granular and the cells are compactly arranged except in the lenticels.

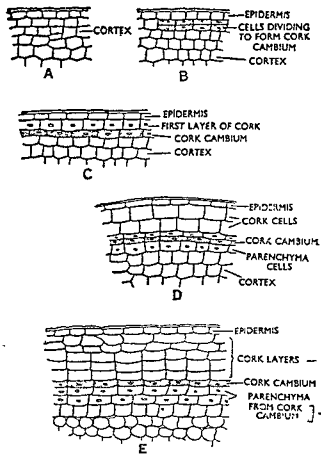


Fig. 10.1. (A—E). Various stages in the development of ... *Prunus*
A—B, The cork cambium or ... lying
below the epidermis. C, The ... evelops
below the epidermis D—E ... side
and the cork layers increase in number.

The phellogen originates at different depths outside the vascular cylinder. In *Pyrus* and *Nerium* the epidermal cells become meristematic,

and give rise to the phellogen. In *Prunus* stem the phellogen arises below the epidermis (Fig. 10.1, A—E). In *Pyrus* the phellogen may arise partly from the epidermis and partly from the sub-epidermal cells. In *Aristolochia, Robinia, Bougainvillea, Boerhaavia, Mirabilis, Pinus,* and *Larix*, the phellogen originates from the second or the third layer of the cortex. It may also arise from cortical cells near the vascular cylinder or from the phloem cells as in *Vitis vinifera, Punica sp., Camellia, Berberis,* etc. In *Aristolochia, Tilia,* and *Robinia,* concentric layers of phellogen develop one after the other. The first one is formed in the epidermis or outermost cortical layer and the rest follow in deeper layers. The last may appear in the phloem. In these cases successive layers of periderm are recognisable outside the vascular cylinder. In the roots of *Vitis* the **phellogen** arises from the pericycle (Fig. 10.2, A).

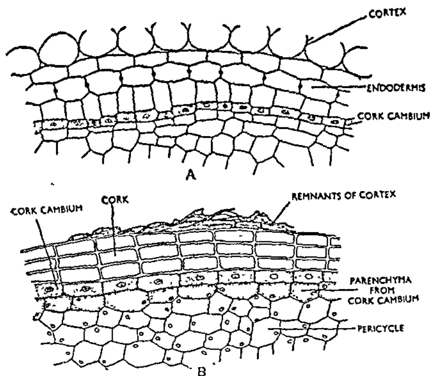


Fig. 10.2. (A—B). A ; Cork cambium being differentiated from the pericycle of the root of *Vitis*. B ; Portion of root of rubber plant showing the cork cambium and the secondary tissues formed by it.

The phellogen may form a complete layer of meristematic cells encircling the axis or it may arise in isolated patches. In ridged stems the phellogen below the ridges is slightly deeper than that below the grooves. In case more than one phellogen layers develop in a stem, the first one is generally parallel to the surface, but the subsequent ones ... two methods of origain ; (*i*) If the first layer is deep-seated the

subsequent ones follow the same course of development and are parallel to the surface, and (*ii*) if the first one is superficial, the subsequent ones arise in different parts of the axis and form discontinuous layers that are not parallel to the surface of the axis but form outwardly curved plates.

[illegible] of meristematic activity of the [illegible]t appears. These cells undergo [illegible] and inner cells. If the outer [illegible]*mbium* the inner cells become [illegible] ones remain meristematic and function as phellogen the outer ones transform into a cork layer. This is the first cork layer (Fig. 10.1, C) or the **phellem.** Further periclinal divisions give rise to more layers of cork cells (Fig 10.1, C—E) towards the outer side, the inner cells function as **cork cambium** or [illegible]

[illegible] **phelloderm** [illegible] layers deep. The number of cork layers formed during one year varies between 2—20. In *Quercus suber* (cork tree) the number of cork layers is much more. The time of initiation of the first layer of **phellogen** varies in different plants.

2. Phellem or Cork Layers. The **phellum** or the cork layers arise as a result of tangential or periclinal division of phellogen cells. The cells cut off towards the outer side, mature into cork cells or **phellem.** These cells are compactly arranged and have thin cellulose walls [illegible] iving mate[illegible] igen-tiall[illegible] sub-stanc[illegible] **suberin** [illegible] n of disti[illegible] ss of the wall varies with species. Suberin is impervious to water. The cork cells may also contain resinous or tanniferous materials in their lumina [illegible] colour to the walls of the cork cells, [illegible] ttle cork, the cavities of cork cells [illegible] makes the cork light in weight. Such cells have comparatively thin walls. The suberin is also resistant to the action of [illegible] es of the cells also gives it th[illegible] of the cork layer make it a[illegible] l also a useful commercial product.

In *Betula* the thin-walled and thick walled layers of cork alternate which each other. In some cases the cork cells also contain sclereids and crystals.

3. Phelloderm A layer or layers of thin-walled cells cut of towards the inner side of the phellogen form **phelloderm** (Fig. 10.1, D—E). The cells of this layer are thin and living and possess cellulose cell walls

depths become meristematic and undergo periclinal division cutting off

storied appearance.

LENTICELS

Wutz (1955) defined a *lenticel as a small portion of the periderm where the activity of the phellogen is more than elsewhere, and the cork cells produced by it are loosely arranged and possess numerous intercellular spaces.* The part of phellogen, producing this loosely arranged group of cells also has cells with intercellular sp
of cells in the lenticels makes them the
lenticels are found in the periderm of bot
are also found on the fruits *e g.*, small dots on the surface of fruits in apples and plums. Lenticels usually occur as raised corky spots on the surface of the main axis and its branches. They are present in most of the plants undergoing secondary growth. *Tecoma radicans, Vitis* are some examples in which no lenticels are
n be attributed to
The peeling off
tissue in contact

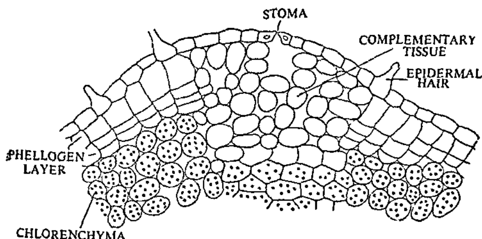


Fig. 10.3. Early stages in lenticel formation. Formation of complementary tissue and lenticel phellogen has taken place.

The *lenticels* generally appear beneath the old stomata or group of stomata or they may appear in-between the stomata. They have also been reported to occur in a position opposite the multiseriate vascular ray, but Wutz (1955) maintains that there is no constant positional relation between the vascular rays and the lenticels.

which have pits. The cells are arranged in definite radial rows. In some species these cells may contain chloroplasts and starch.

Bark. Esau defines the bark
that are found external to the se
includes the pericycle, cortex,
external to the periderm. In cas
part of the cortex or from the epidermis, the term bark can be applied to all the tissues lying external to
periderm including the perider
the phloem itself the cells externa
a loose term and is considered to

In *Quercus suber*, *Corpinus* and *Fagus sylvaticus*, the cork cambium remains active throughout the life of the plant. In these cases the first layer of cork cambium appears immediately below the epidermis and after producing periderm tissues it becomes inactive. The second layer appears in the middle of cortex and the third below it and like this successive layers of cork cambium appear in deepes tissues like the pericycle and secondary phloem and produce the periderm tissue. In such cases the living and dead tissues external to wood are all of
as bark. These tissues are cut off
and hence the bark is no longer
expansion of the stem or the root.
tree is old, it is either shed or it
becomes longitudinally fissured. As a result the outer part of the phloem is shed with the bark. So in old trees the layer of phloem

shed by the formation of abscission layers. In some cases a layer of thin-walled cells is laid down by the cork cambium amidst the thick-walled or suberised cork cells. These thin-walled cells are called abscission layers. Under the effect of moisture on these layers and by the tension set up by the increasing diameter of the stem the bark splits and is sloughed off.

Wound periderm. It originates only when a plant part is wounded. As a result the cells that are injured die. Below this layer of dead

phellogen

phelloderm

and Fungi.

Periderm in monocots. Some monocots, like *Aloe*, *Coconut palms*, *Royal palms*, *Cordyline terminalis* etc ; produce periderm tissue. In these cases the parenchyma cells of the ground tissue lying at various

depths become meristematic and undergo periclinal division cutting off new cells that are arranged in radial files. These cells become suberised and form cork layers that are protective in function. The regular arrangement of the suberised cells in distinct rows gives the cork a storied appearance.

LENTICELS

Wutz (1955) defined a *lenticel as a small portion of the periderm where the activity of the phellogen is more than elsewhere, and the cork cells produced by it are loosely arranged and possess numerous intercellular spaces.* The part of phellogen, producing this loosely arranged group of cells also has cells with intercellular [illegible] of cells in the lenticels makes them th[illegible] of [illegible] small dots on the surface of fruits in apples and plums. Lenticels usually occur as raised corky spots on the surface of the main axis and its branches. They are present in most of the plants undergoing secondary growth. *Tecoma radicans, Vitis vinifera, Philadelphus*, etc., are some examples in which no lenticels are [illegible]

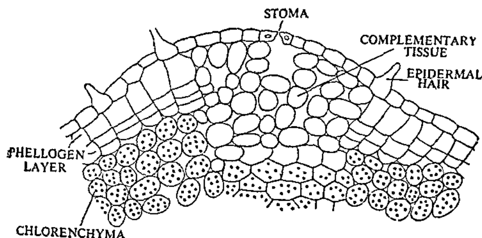


Fig. 10.3 Early stages in lenticel formation. Formation of complementary tissue and lenticel phellogen has taken place.

The lenticels generally appear beneath the old stomata or group of stomata or they may appear in-between the stomata. They have also been reported to occur in a position opposite the multiseriate vascular ray, but Wutz (1955) maintains that there is no constant positional relation between the vascular rays and the lenticels.

In the dicots, Wutz (1955) recognised three types of lenticels :—

1. In this type (Fig. 10.4, A) the complementary tissue is made up of cells that appear to be compactly arranged, but possess intercellular spaces. This type is characteristic of *Salix*, *Pyrus*, *Populus Malus*, *Magnalia*, *Liriodendron*, *Ginkgo*.

2. In this type (Fig. 10.4 B) the complementary tissue is composed of thin-walled and unsuberised cells, that are loosely arranged *e.g.*, *Fraxinus*, *Quercus*, *Sambucus*, and *Tilia*.

3. In this type (Fig. 10.4, C) the complementary tissue shows distinct layers of one or more cells deep, of suberised cells and loosely arranged unsuberised cells. The suberised cells are compactly arranged and serve to hold together the tissue. They are called **closing layers** (Fig. 10.4). Formation of new cells beneath exert pressure on the earlier formed tissue and results in the rupture of the closing layer (Fig. 10.4)

LENTICELS AS ROOT BUDS

Van Mohl (1832, pp. 65—74) raised a question in one of his articles in Flora. "Are the lenticels to be regarded as root buds ?"

In the year 1826 Candolle observed the formation of a group of inflated parenchyma cells in the lenticells of some woody tress. He also observed that a
groups of cells.
Devaux (1900, I
(1964) described the formation of hyperhydric tissue and development of adventitious roots in the lenticels of many woody trees. Recently Chen Ginzburg (1967, pp. 4—8) described the development of such roots from the lenticles of *Tamarix aphylla*. He has described the organisation of the adventitious root apex and its further growth. He observed the following changes :—

(*a*) A group of cells in the hyperhydric tissue of the lenticels become meristematic.

(*b*) Cells divide at random.

(*c*) A stage at which majority of cells divide in a transverse plane with respect to the axis of the primordium.

(*d*) Formation of **procolumella.**

(*e*) Differentiation in the primary meristems of three regions of the root.

(*f*) The promeristem enlarges.

(*g*) The root primordium emerges from the hyperhydric tissue.

(*h*) The procambial strands of the adventitious root become conected with those of parent organ.

T
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Origin and structure of lenticels. Initiation of the lenticel below the stoma is marked by the division of some cells below the stoma in different planes to form a mass of rounded cells (Fig. 10.3). These cells grow bigger in size, lose their contents, and become colourless. They form first layer of **complementary cells** (Fig. 10.3). Beneath these cells the **phellogen** or the cork **cambium** makes its appearance. Its cells divide tangentially and cut off more complementary cells

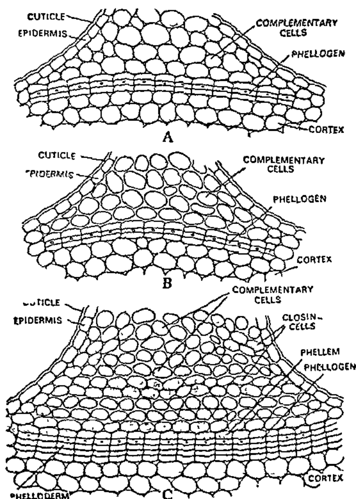


Fig. 10.4. Lenticels. A, T.S. lenticel of Saliv B, T.S. enticel of *Quercus* C, T.S. lenticel of *Prunus avium*.

towards the outer side. The **phellogen** in the lenticel region characterised by the presence of intercellular spaces between its cel As the new complementary cells are added towards the outer side, t overlying epidermis ruptures and exposes the underlying complemen ary cells (Fig. 10.4). The complementary cells are thin-walled ar are loosely arranged.

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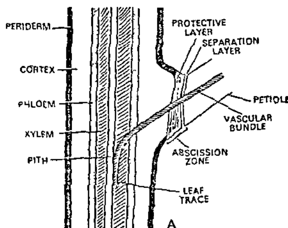
(*h*) The procambial strands of the adventitious root become conected with those of parent organ.

These studies clearly indicate that this phenomenon of formation of adventitious roots from lenticular hyperhydric tissue is of great advantage to the plants in their vegetative propagation under natural habitats.

These later studies have, to a greater extent, answered the question raised by Van Mohl in 1832.

ABSCISSION

Abscission is a common phenomenon in the vascular plants. It consists in the separation of leaves, bracts, floral parts, fruit and foliage branches from the plant. The separation does not involve wounding or injury to the plant. The surface exposed as a result of abscission



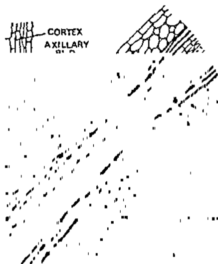


Fig. 10.5. Leaf abscission in Angiosperms.

is already covered with a protective corky layer, called the **protective layer**. This layer is present next to the abscission layer.

Abscission of Leaves. In the pteridophytes and some herbaceous angiosperms (mostly monocots), the leaves die on the plant. In majority of the woody angiosperms and gymnosperms, the leaves fall ... they die. *This separation of the leaves from the branch, without*

causing any injury is called leaf abscission. It is effected by the formation of an abscission zone (Fig. 10 5) at the base of the petiole. This zone is differentiated by certain cytological and chemical changes in the cells along which the leaf will separate. This region or the abscission zone is made up of two distinct layers : (1) the abscission layer or the separation layer ; and (2) a protective layer which occurs below the abscission layer.

Addicot and Lynch (1955, pp. 211—238) have described three kinds of dissolution phenomena that occur in the abscission layer and result in the separation of leaves : (1) the middle lamellae in the abscission layers dissolve and result in leaf fall ; (2) in addition to middle lamellae the primary wall also dissolves : (3) all the cells of the abscission layer dissolve and cause leaf fall.

Sacher (1957 pp. 1199—1200) observed that the cell membranes of the abscission layer lose their property of differential permeability and the intercellular spaces between the cells become filled with a liquid. This leads to ultimate dissolution of the cells.

Sequira and Steeves (1954) state that the leaf fall in Coffee is due to an infection by a fungus called *Omphalia flavida* which causes auxin destruction by producing Indol acetic acid auxinases and causes the formation and dissolution [illegible]
when Indol acetic acid is sup[illegible]
and Hall (1962) also conclud[illegible]
acceleration of development of abscission layer in cotton leaves. The plants of *Begonia*, *Fuchsia* and *Coleus* have been reported to shed their leaves as a result of subjection to poor illumination (Molisch). *Mimosa pudica* has been shown experimentally to shed its leaves when subjected to tobacco smoke for 24—48 hours.

The dissolution of the middle lamellae or the entire cells, or the accumulation of liquid in the intercellular spaces of the abscission layer occur only in the tissue surrounding the vascular region. After the dissolution of abscission layer the leaf is held by the vascular region. The formation of tyloses in the vessels stops water supply to the leaf. A little disturbance to the leaf by wind or any other mechanical pressure (weight of the leaf lamina, etc.) causes the break of vascular tissue and the leaf falls.

Scott, Webster, Miller and Leopole (1967, pp. 730—734) studied certain anatomical changes that occur during leaf abscission in *Phaseolus vulgaris* L. They observed that as the leaf approaches senescence and abscission, there is an alteration in the appearance of vascular elements [illegible]
of tyloses in the [illegible]

[illegible] formation of tyloses in xylem vessels induces a water stress in tissues distal to the separation zone. The callose plugs in the sieve elements were seen to disappear as abscission

proceeds. This resulted in the increased movement of nutrients from the distal parts of leaf towards the petiole. This depletes the cells, of their nutrition and results in the senescence of tissue. So water stress and senescence in the distal regions hasten the rate of cellular senescence in the zone of separation.

As a result of leaf fall the exposed cells form a protective layer by depositing lignin and suberin on their walls and in the intercellular spaces. This protective layer is soon replaced by periderm which develops below the protective layer.

The floral parts may also abscise in different stages of development. Their abscission is also brought about by the formation of a separation layer. This layer may develop by the division of cells at the base of the floral organ, or the cells may differentiate into a separation layer without undergoing any division. Dissolution of the middle lamellae or the primary walls of separation layers bring about the abscission.

The fruits also develops separation layers which cause abscission.

11

THE ROOT

The root is a typical feature of the sporophytes of vascular plants. It develops, from th[illegible] usually called the radicle. Durir[illegible] first and comes out of the seed [illegible] ot of the plant. Such a root i[illegible] th[illegible] so[illegible] ro[illegible] ac[illegible] Tl[illegible] and storage.

Normally, the roots grow in soil, but aerial roots are produced in Banyan, Ivy, some vines and some epiphytes. Their function is also anchorage and absorption of water, or moisture from the air.

PRIMARY STRUCTURE OF THE ROOT

[illegible] into nc[illegible] ws a [illegible] A tran[illegible] lemarc[illegible] cortex and the vascular tissue system. The pith may or may not be present. The root cap, if present, also forms a part of the primary body of the root.

DICOT ROOT

A cross-section through a dicot root in the primary state of growth shows the following tissues from outside within :

Epidermis. It is an external layer of tightly joined cells that are devoid of stomata. This layer is usually [illegible] rhizodermis. I[illegible] of cell elongation possess tubular and unicellular extensions called the root hair (Fig. 11.1). They increase the absorptive surface of the root and also function as water and solute absorbing structures. In some cases the epider[illegible] are smaller in s[illegible] and bigger in s[illegible]

The root hair are generally short-lived but in some cases they have been reported to live longer.

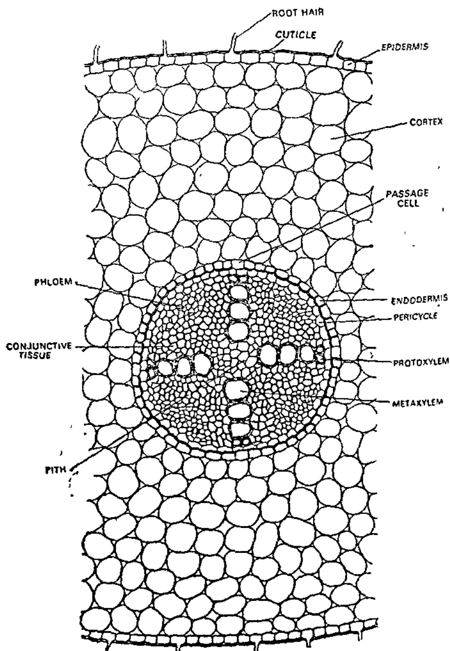


Fig. 11.1. T.S. root of gram (dicot.) Note tetrarch xylem and a small pith in the centre.

In some herbaceous perennials, the epidermis is long-lived and acts a chief protective tissue (Luhan 1955 pp. 87—92). In such cases the

walls of epidermal cells become thickened. The root epidermis is now known to be covered by a distinct cuticle (See Scott, Hamner and Bowler, 1958).

Exodermis. This layer is present below the epidermis (*Citrus*, Cossman, 1940) and is often regarded as a protective layer. It arises from one or several of the sub-epidermal layers of the cortex. The ... h ... and ... ster ... of ... walls. The suberin lamellae develop on ... plasmic contents ... (1950) recorded ... The exodermis is present in most of the monocot roots and in some dicot and gymnosperm roots. It is absent in the vascular cryptogams. It varies in thickness from one to several layers.

Cortex. The cortex in the roots is comparatively simple in histology ... with losts of inter- ... spaces are large ... nae develop by breaking down of cells. The arrangement of cortical cells sometimes shows distinct patterns, In some cases, they are arranged in distinct radial rows, whereas in others the cells show concentric layers with cells in each layer alternating with others, (Fig. 11.1). In some her- ... dary growth, the cortex is perma- ... rious types of mechanical tissues. ... tical cells of the roots, but they store ... *ospora*, the chloroplasts are present in

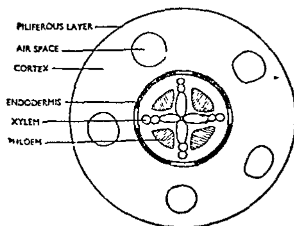


Fig. 11.2. Diagrammatic T.S. through a dicot tetrarch roots (Sunflower).

In the roots of *Launea nudicualis*, the cortex is traversed by laticifers (latex cells). In most of the dicots, the cortex is replaced by

tains continuity by the anticlinal divisions of its cells. In the young root of *Helianthus annuus* the endodermis in part may be biseriate and in part may be uniseriate and the two conditions alternate in the endodermal ring (Daniel and Hillson, 1973).

The Vascular Cylinder. The layer next to the endodermis is generally pericycle. It constitutes the outer boundary of the primary vascular cylinder of the dicot roots. The pericycle may be uniseriate or

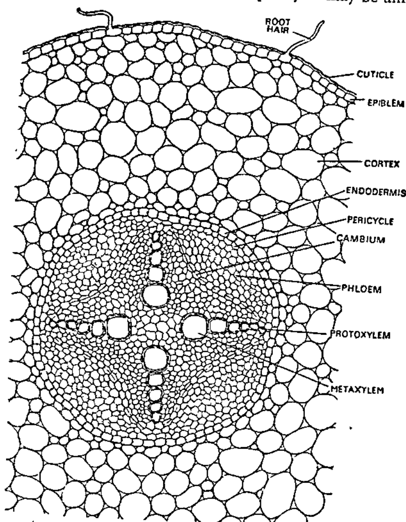


Fig. 11.4. T.S. root of gram. Note tetrarch xylem and formation of cambial strips

multiseriate (*Morus*, *Salix*, aerial roots of *Ficus benghalensis*). It is generally composed of thin-walled cells. In *Salix* the many-layered pericycle is made up of thick-walled cells
a few water plants the pericycle is abse
quite early in the histogenesis of the r
bial strands. It retains its meristemat

suberised cells as a result of secondary growth. In Pear the cortical cells outside the endodermis have collenchymatous thickenings (Guttenberg, 1940). Presence of reticulate thickenings in the cell walls of cortical cells immediately next to endodermis have been reported in the members of *Cruciferae*, *Rosaceae* and *Caprifoliaceae*.

Endodermis *It is a distinct layer of cells differentiated from the innermost layer of cortex.* The layer is of universal occurrence in the roots and is uni ... d by the presence of ... 11.3) and transverse ... nings of suberin (Fig. ... cell. This band is a part of the primary wall. It is actually a continuous

Fig. 11.3. T.S. root of *Helianthus annuus* (dicot). Note tetrarch xylem. There is no pith.

band of chemically modified wall substance. Cytoplasm of the endodermal cells is in firm contact with the casparian strips. This firm relation between the cytoplasm and casparian strips is not without significance. ... materials in the root and ... ent can only be effected t ... because movement ... presence of suberised caspa... destroyed after the secondary ... growth endodermis main-

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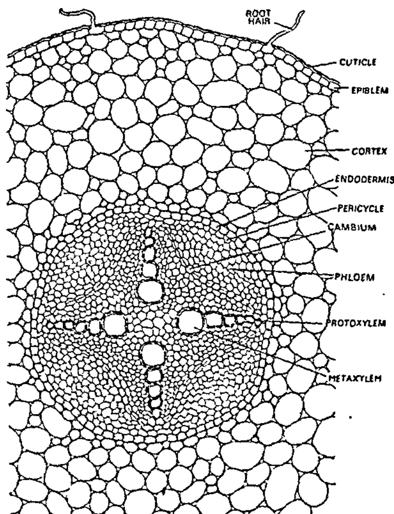


Fig. 11.4. T.S. root of gram. Note tetrarch xylem and formation of cambial strips

multiseriate (*Morus*, *Salix*, aerial roots of *Ficus benghalensis*). It is generally composed of thin-walled cells. In *Salix* the many-layered pericyle is made up of thick-walled cells. In some parasitic dicots and a few water plants the pericycle is absent. The pericycle differentiates quite early in the histogenesis of the root and arises from the procambial strands. It retains its meristematic potentialities to a remarkable

degree and gives rise, by the activity of its cells, to lateral root primordia, phellogen, and portions of vascular cambium.

The Vascular Tissue. The arrangement of primary xylem and primary phloem is characteristic in the roots. In striking contrast to the collateral arrangement of the [illegible] is alternate and radial in the [illegible] the xylem but it alternates [illegible] In a transverse section the [illegible] appear as separate bundles or plates of tissue with strips of parenchymatous cells in-between them. The number of xylem and phloem strands that alternate with each other differs in different plants. It may vary [illegible] the roots are desig- [illegible]

in *Pisum*. In *Helianthus*, *Cicer*, *Vicia*, *Gossypium* and *Ranunculus* the roots are tetrarch There are some dicots in which the root of the same plant shows diarch, triarch and tetrarch xylem, (Just, 1232, Torry, 1957). Wardlaw (1928) reported tetrarch and polyarch roots in *Nymphaea chilensis*. Banerji (1932) reported tri-arch, tetrarch and pentarch roots in *Enhydra fluctuans*. Such roots are called **hetro-archic roots.** In *Helianthus annus* the root is diarch about 1·5 mm. behind the root tip. It becomes triarch at 1·6-mm. level and *it becomes tetrach at* 2·0 *mm.* level. This condition arises by the appearance of procambial cells in-between the two phloem groups. These procambial cells separate the phloem group into four groups. The procambial cells *differentiate* into primary xylem thus making four xylem strands. The xylem strands possess earlier formed tracheary elements or protoxylem and later formed tracheary elements called the metaxylem. The **protoxylem** elements lie next to the pericycle and are smaller in size. They have spiral annular, reticulate and scalariform thickenings. The **metaxylem** elements are wider and are present towards the centre. Their walls generally possess bordered pits. Thi[illegible] of the xylem in roots is called **ex**[illegible] of the roots, the pith is ab[illegible] two types of tracheary elements *i.e.*, the tracheids and the vessels. [illegible] *vessels generally appear polygonal in a cross-section. The protoxylem* elements are fewer in number and in most cases it is represented by a single vessel.

The phloem consists of sieve-tubes, companion cells and phloem parenchyma. The protophloem occupies the peripheral position and [illegible] inner side *i.e*, the *development* [illegible] companion *cells in the dicot roots* [illegible] and are usually absent in the protophloem.

The parenchyma cells between the xylem and phloem strands form a tissue called the **complementary tissue.** Most of the cells of this tissue differentiate into vascular cambium. Phloem fibres have been

reported to be absent in the primary roots. Their presence has, however, been reported in the primary phloem of some members of the familes *Annonaceae*, *Malvaceae* and *Papilionaceae* (Guttenberg 1943). In *Vicia faba*, phloem fibres are well-developed in the primary phloem.

MONOCOT ROOT

The monocot roots differ from the dicot roots in the absence of secondary growth.

Epidermis. The structure of the epidermis is similar to that of dicot root and is composed of closely packed elongated cells that are covered by cuticle. Scot, Hammer and Bowler (1858) have shown the presence of cuticle on the epidermis of *Allium cepa*. It is generally

velamen

roots of orchids functions as a protective layer and reduces the loss

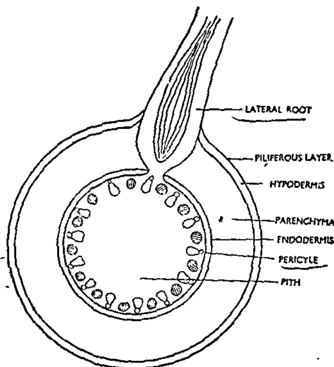


Fig. 11 5. Diagrammatic T. S. through root of maize (Monocot) showing a lateral root.

of water ... attribute ...

like or reticulate ...

pneumatodes ... They help in

gaseous exchange. Gessner (1956) reported that the endodermal cells that are in contact with the cells of the pneumatodes are filled with air. Below the epidermis, there are generally present one or more layers of **exodermis**.

Cortex. It is made up of several layers of cells that have lots of intercellular spaces between them. In maize, some layers of cortex below epidermis are made up of thick-walled cells (Fig. 11.6). These layers are often distinguished as **exodermis.** They develop suberised secondary walls, but differ from cork cells in possessing living cell contents. In the tuberous roots of *Asparagus* the cortex is extensively developed and can be distinguished into three regions Fig. 11.10.

(*i*) *Outer cortex*, which is made up of smaller thin-walled cells.

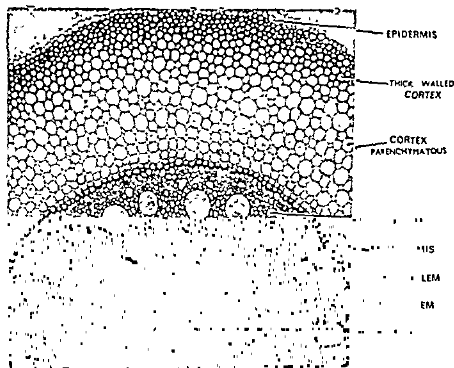


Fig. 11.6. Microphotograph of T.S. of monocot root of maize.

(*ii*) *Middle cortex*, which is composed of large parenchymatous cells that make up the storage region of the root. This region is extensive and well-developed.

(*iii*) *Inner cortex*, which is made up of a few layers of thin-walled cells of smaller diameter.

In the roots of water plants (*Hydrilla* 11.14 ; *Potamogeton, Typha* etc. and *Oriza sativa* (Fig. 11.11) the cortex is traversed by large air spaces or lacunae. Such a cortex is called **lacunate.** The cortical cells in *sativa* are arranged in distinct radial files (Fig. 11.12).

Endodermis. It is the innermost layer of cortex and is characterised by the presence of **casparian strips** on both the radial and transverse walls. In most of the monocots *e.g., Maize, Bromus* 'grass etc., the radial and the inner walls are extremely thick as compared to the outer walls (Fig. 8.24 A). These thickenings of the inner walls of endodermal cells is due to the development of a lamella of suberin. At a later stage of development this suberin lamella is covered by a layer of cellulose which in some monocot roots attains a considerable thickness. Lignification of these walls of endodermis has also been reported. These thickening materials appear first in the endodermal cells that are opposite the phloem. From here they spread to the other endodermal cells. Here and there some cells of the endodermis remain

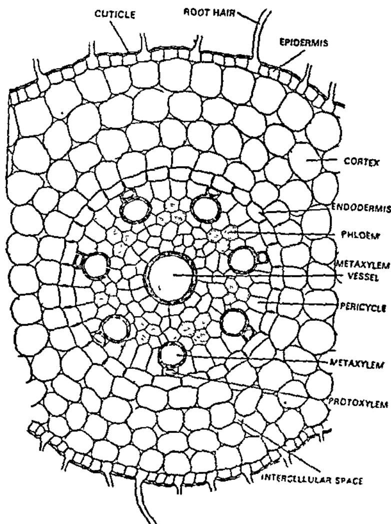


Fig. 11.7. T.S. Monocot root of *Hordeum vulgare* (Barley)
Note the presence of central metaxylem vessel.

thin-walled and are called **passage cells.** They allow radial diffusion of water. The passage cells may remain thin-walled throughout the

life of the root or, in some cases, they may also become thick-walled. It resembles the endodermal layer of dicot roots in all respect.

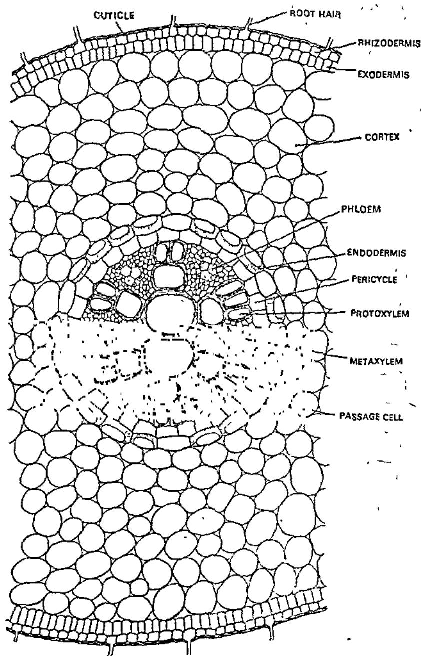


Fig. 11.8. T.S. Root of *Allinm cepa* (Monocot).

Pericycle. It is usually uniseriate and is composed of a single layer of thin-walled cells. In maize it may be a multiseriate parenchymatous tissue. In *Smilax*, the multiseriate pericyle is composed of

thick-walled cells (Fig. 11.13). Pericycle is generally a complete ring of cells but in some grasses its continuity is interrupted here and there by protoxylem elements. Its function is to give rise to lateral roots.

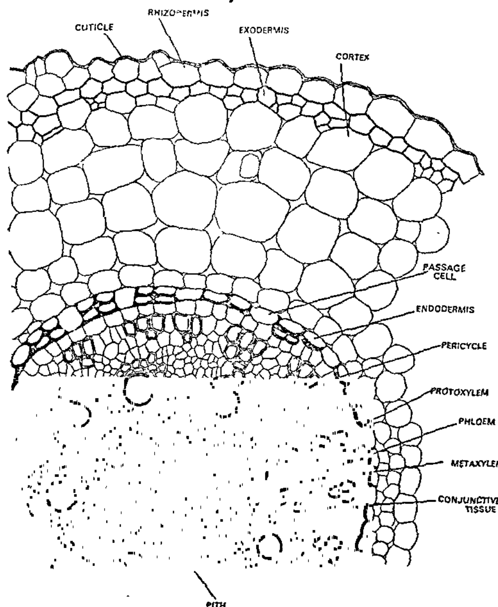


Fig. 11.9. T.S. root of grass.

Vascul[illegible]

strands of [illegible]

plants. I[illegible]

sclerenchymatous in the root of *Typha*. In *Triticum* and *Hordeum vulgare*,

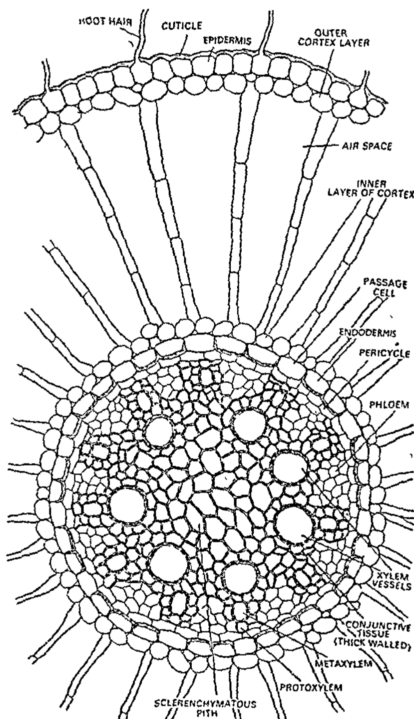


Fig. 11.11. T.S. root of *Oriza sativa* (Rice). From a specimen collected under aquatic conditions. Note sclerenchymatous pith.

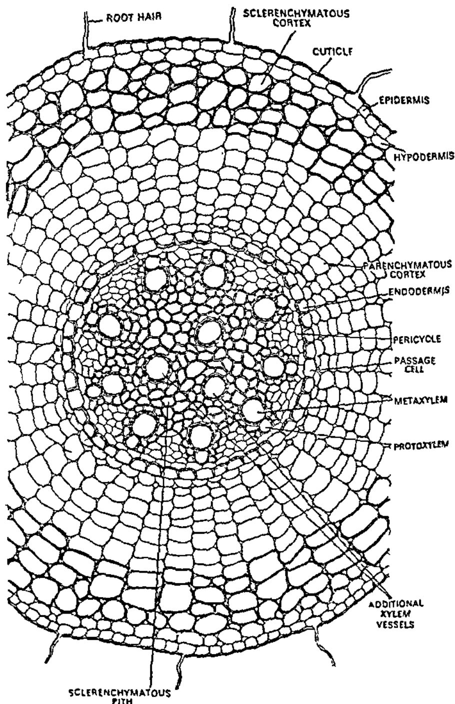


Fig. 11.12. T.S. Root of *Avena sativa* (Monocot). Note sclerechymatous pith and additional metaxylem vessels. The cortical cells are arranged in distinct rows,

the centre is occupied by one large metaxyem vessel (Fig. 11.7). In *Allium cepa* (Fig. 11.8) the xylem is hexarch with two metaxylem elements in the centre. The pith is absent in this case. In grasses *(Fig. 11.9. the xylem is polyarch and distinct pith is present. In Avena* *sativa* (Fig. 11.12), there are 1—3 additional metaxylem vessels in the centre.

[illegible] xylem elements are [illegible] towards the inner [illegible] meter and the walls [illegible] thickening. The number of protoxylem elements is more than one and form an outer ring of xylem alternating with protophloem elements. The metaxylem vessels occur towords the inner side and have larger diameter. The innermost vessels of metaxylem are large and generally spherical or oval in shape in a transverse section (Eig. 11.6). The walls have pitted thickenings.

[illegible] this tissue. In *Zea mays* each sieve element of the protophloem is accompanied by two phloem parenchyma cells that resemble the [illegible] starch grains.

Root Cap. The root cap is present at the tip of the root and is [illegible] walls of the cells of the root cap near its periphery and those next to the root tip have mucilaginous consistency. The root caps are always present in the plants growing in soil and may be present or absent in the roots of water plants. Sometimes, the roots growing in soil do not develop root caps when made to grow in water cultures.

Root Hair. [illegible] new root hair bring them in contact with new soil. The root hair may

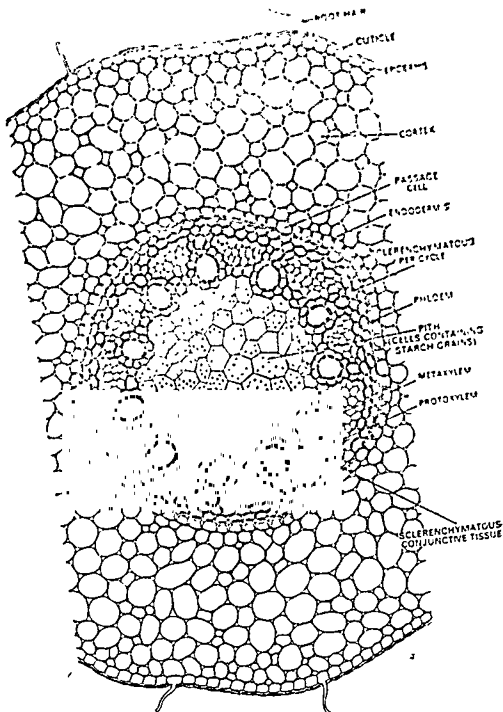


Fig. 11.13. T.S. root of *Smilax* (Monocot). Note the sclerenchymatous pericycle.

be absent in some water plants. Sometimes, the plants which normally have root hair do not develop them, if grown in water.

The root hair are unicellular and arise as small or long protuberan- ... ances ... and ... the root hair and forms a lining layer enclosing a large central vacuole.

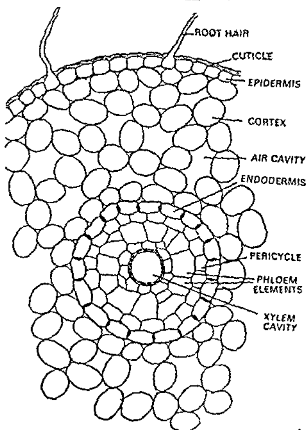


Fig. 11.14. T.S. root of *Hydrilla*. Note air-spaces in cortex and a single xylem cavity.

... of the root ... cylindrical ... obstacles. They assume a tortuous course of development in hard soils.

Mycorrhiza. In some c... association with a fungus. ... hair are absent in most of the ... is performed by the fungal hyphae.

In Leguminous plants the roots develop tubercles or nodules. These nodules arise as a result of *hypertrophy* induced by *nitrogen-fixing* bacteria which live in the cells of these roots. The bacteria get shelter and food from *host roots* and in turn fix free nitrogen for the plant. Such an association is called **symbiosis.**

Lateral Roots. The lateral roots or the branches of the roots have a deep-seated origin and are, therefore, said to have an **endogenous origin.** In the seed plant, *they always arise from the* **pericycle** whereas in the pteridophyta they originate from the endodermis. In the diarch roots the lateral roots arise *from* the region of the pericycle between the phloem and xylem bundles (Fig. 11.15). In the triarch, *tetrarch*, pentarch roots the lateral roots arise opposite the xylem bundles (Fig. 11.15). In the polyarch roots, the *lateral* root arises opposite the phloem bundles (Fig. 11.15).

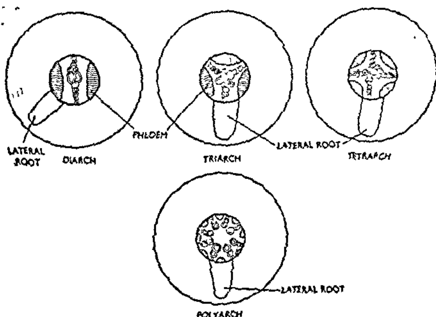


Fig. 11.15. Different patterns of position of lateral root with respect to *the xylem* and phloem of the main root.

[illegible] is marked by the periclinal *divi*sion [illegible] These divisions are followed by [illegible] resulting in *the formation* of a small protuberance. *It is the* [illegible] root primordium (Fig. 11.16). The endodermis is either *crushed* by the growing primordium or its cells divide anticlinally and keep pace with the *growth.* The primordium increases in length and pushes its way through the cortex and [illegible] out on the surface of the roots. The cells of the [illegible] front of the growing *tip.* The root [illegible] growing lateral root develop when it is [illegible] 11.17). The vascular tissues and the

cortex also develop behind the promeristem. The vascular tissues of the lateral root become connected with the vascular elements of the main root through the cells of the pericycle which become differentiated into these elements.

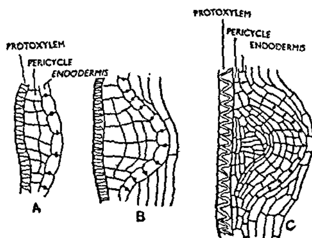


Fig. 11.16. A—C. Various stages in the origin of the lateral root from the pericycle.

Adventitious Roots. The roots which do not develop from radicle are termed as adventitious roots. Such roots arise from the stem (both aerial or underground) and its branches; from the leaves and from the older roots. The lower vascular plants (Pteridophytes) have their root system composed entirely of adventitious roots ... f monocots, saprophytic ...

The adventitious roots generally have a deep-seated origin *i.e.*, they are **endogenous.** Mostly, they originate close to the vascular tissue and the young primordi... ...rlying tissue. They generally origi... ...primary phloem which lies ... nonf... ...

... to the development of ... roots.

SECONDARY GROWTH IN THE ROOTS

Foll... ...here is usually a continuous grow... ...seed plants during their life-

separate strips of cambium. In a diarch root there are two such separate strips. These strips become continuous laterally as a result of tangential division of pericyclic cells external to each protoxylem pole. They are forerunners of the cambial cells, although they have enlarged somewhat and have more or less changed in shape, but retain

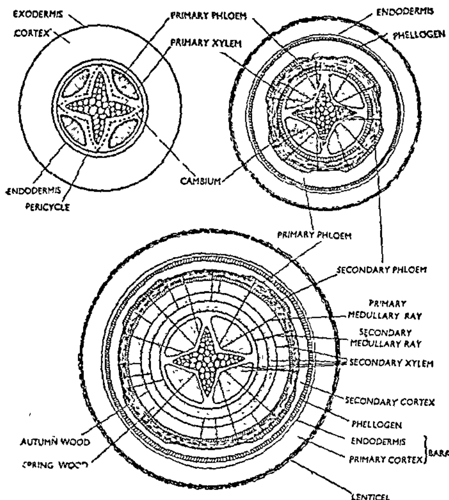


Fig 11.18. Diagrammatic representation of the various stages in the secondary growth of the root of a dicot.

their meristematic capacity. Each of these cells divides tangentially (in a plane at right angles to the radius of the root) into two daughter cells. At least one of these daughter cells enlarges somewhat and divides again. Once started, this activity is now repeated indefinitely. In other words, the beginnings of a new meristem are now established between mature primary tissues. As the ... the cam- ... mature ... tivity re- ... y xylem

elements. The cells that are cut off towards the outer surface of the cambial strips mature into elements of secondary phloem, which are, therefore, located between the cambium and the inner face of primary phloem strand. As a result of this activity of the cambial strips, collaterally arranged strands of secondary vascular tissue are built up between the ad acent primary xylem plates (Fig. 11.20.)

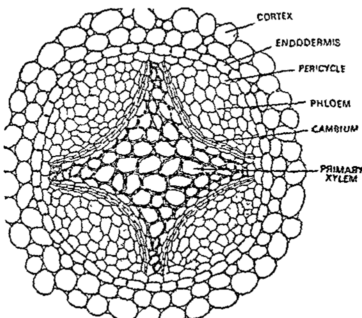


Fig 11.19. T.S. dicot rool at a stage at which cambial activity is beginning (diagrammatic).

Rays. The secondary xylem and the secondary phloem elements produced as a result of the activity of the vascular cambium are, however, not in the form of a complete ring. Here and there the cambial cells destined to give rise to secondary xylem elements and secondary phloem elements remain undifferentiated and parenchymatous. As a result, radiating plates of parenchymatous cells result, which are known as **rays.** In many roots, those portions of the cambium external to the protoxylem groups function as **ray initials** and give rise to **multiseriate rays** (Fig. 11.22), in addition to those produced elsewhere in the circumference of the cambium. With the enlargement ofvascular cylinder, the number of rays also increases.

As a result of the more rapid development of tissues between the primary xylem strands, the cambial cylinder assumes a circular outline in a transectional view (Fig. 11.23).

Secondary Xylem and Phloem. The organisation of the secondary xylem varies in various plants. Some plants contain a greater portion of conducting elements, which are only tracheids in the

gymnosperms, only vessels in willow, and both tracheids and vessels as in *Oak* and other dicots. Elements other than tracheids and vessels may also form the bulk of secondary xylem. Such elements are thick-walled mechanical cells that are not concerned with conduction. These thick-walled cells contribute to the efficiency of the root as an

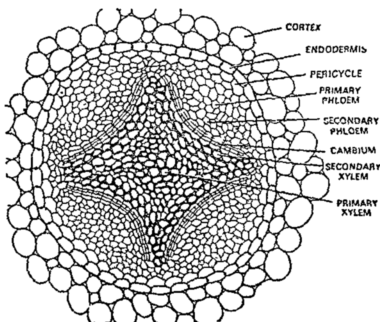


Fig. 11.20. T.S. dicot root at a stage at which secondary xylem and secondary phloem have begun to be formed.

organ that anchors and supports the stem. In some storage roots, the secondary xylem consists of storage parenchyma.

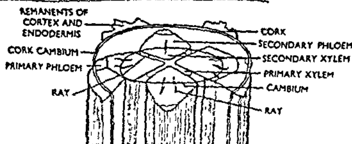


Fig. 11.21. Three-dimensional diagram of a portion of a dicot root after considerable secondary growth.

[illegible] ation by repeated tangential divi- [illegible] irst formed elements of secondary [illegible] arranged in definite radial rows. In most of the gymnosperms such as *Pinus*, this radial arrangement of the secondary elements is retained as they do not undergo much enlargement during the course of their maturation. In sun-flower, vessels of the secondary wood undergo considerable enlargement as

compared to other xylem elements. As a result, the various elements of the secondary xylem become irregularly disposed.

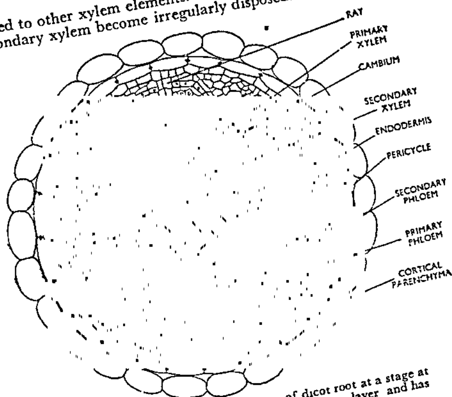


Fig. 11.22. T.S. of stelar region of dicot root at a stage at which cambium has become a continuous layer and has produced considerable amount of secondary tissue.

Annual Rings. In the perennial trees, shrubs, and woody climbers (vines), the formation of secondary xylem and phloem continues year after year. In such cases the xylem elements differentiated in the beginning of each season's growth are comparatively large and thin-walled as compared to those that differentiate with the advancing season. In *Willow* the vessels differentiated in the spring season (spring wood) are larger in size and those that are formed later go on becoming smaller and smaller and possess thick walls. The vessels formed towards the close of the season are the smallest and possess very thick walls (autumn wood or summer wood). In late summer the formation of vessels by the cambium ceases. The spring wood and the summer wood which form a cylindrical layer of secondary xylem during one season's growth constitute an **annual ring**. During the next growing season the cambium again produces new secondary xylem with first formed spring wood and after formed summer wood. As a result, a transverse section of a mature root shows a clear differentiation between the small thick-walled xylem vessels of the previous year's summer wood and the large thin-walled vessels of the spring wood of the next year's growth. This is the explanation of the occurrence of concentric annual rings that can be clearly seen in a transection of roots of many trees and shrubs.

[illegible] is absent or less clearly marked [illegible] rings in the secondary phloem [illegible] enlarging cylinder of xylem and phloem within crushes it against the encircling tissues.

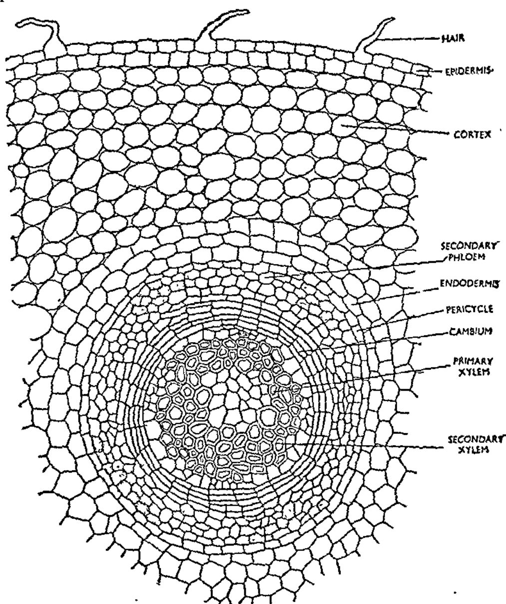


Fig. 11.23. T.S. root of gram showing secondary growth at a stage, where cambium has become circular in outline and has produced sufficient amount of secondary tissue.

Cork and Cork Cambium. The pericycle layer in the roots that show secondary growth retains the ability to divide. When secondary growth in a root is extensive, the primary phloem, endodermis and the

cortex become crushed and are eventually sloughed off. This initiates the formation of a new cylinder of **cork cambium** which arises as a result of the tangential division of the cells of the pericycle (Fig. 11.24). The activity of cork cambium, instead of producing xylem and phloem, produces cork cells to the outside and cork parenchyma to the inside.

The protoplast of the cork cells secretes a fat-like substance, called the **suberin** which is deposited in the cells. This is called **suberisation** and, as a result, the protoplasts of the cork cells die, so that the functional cork is actually a layer of dead cells. These layers of suberised cells (cork layers) that are formed deep within the root (*i.e.* just inside the ruptured endodermis) are impermeable to water and

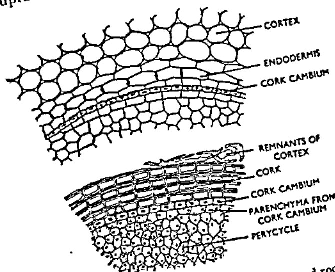


Fig. 11.21. T.S. portions of grape root above and root of rubber plant below showing cork cambium, cork, and parenchyma form cork cambium.

other dissolved substances. This leads to the ultimate death of the cortical and the epidermal cells. These dead cells form the bark and are eventually sloughed off. So the older portions of the roots in such cases are derived entirely from the stele.

In many roots the cork cambium initiates in the cortex and in such cases the older parts of the root are not derived entirely from the stele. Ordinarily, as expansion of that part of the root inside the cork cambium continues, new cork cambium layers are formed to the inside of the old cork cambium from adjacent parenchymatous cells. Soone or later, the outer most cork layer will crack longitudinally and b discarded. New layers of cork are continuously being added ,in th old roots because new cork cambium layers are successively develop inwards from the current cork cambium.

SECONDARY GROWTH IN T[illegible]

In the primary roots of *Bo*[illegible] stelar cambium differentiate betw[illegible] soon appear as two arcs. Stela[illegible] pericycle cells opposite the protc[illegible] plete stelar cambium in the primary root. Secondary growth is effected by a special **primary thickening meristem** that differentiates in the pericycle. Initially, periclinal divisons occur randomly in the cells of the pericycle at the base of the primary root in 6-day old seedlings. In a few days the primary thickening meristem forms a continuous meristematic ring inside the endodermis. This meristematic ring cuts off [illegible] de. In this con- [illegible] These groups [illegible] ondary phloem [illegible] its inner sides. [illegible]

sites secondary phloem can differentiate towards the outer side of the primary thickening meristem in the external conjunctive tissue and secondary xylem to the inside in the internal conjunctive tissue. Subsequently, new arcs of primary thickening meristem differentiate in the outermost phloem cells of these areas and become continuous laterally with the portions of primary thickening meristems that lie on each side of the new desmogen strand. Both these methods can be seen in the same transverse section.

STORAGE ROOTS

The storage roots that are generally the combinations of hypocotyl and root exhibit a great variation in their secondary structure. The anomalies met with in them are an adaptation to their function of storage. Among the dicotyledons some genera of the families *Umbelliferae*, *Chenopodiaceae*, *Convolvulaceae*, *Compositae*, *Cruciferae* etc., afford good examples of the anomalies exhibited by the storage roots.

A few selected examples will suffice to explain the variations in the secondary structure of the storage roots.

Beta Vulgaris (*Chenopodiaceae* ; Figs. 11.25 and 11.26). The [illegible] lescribed in detail by Artschwager [illegible] chwager and Starrett, 1936), and [illegible] this plant is diarch (Artschwager, 1926).

The secondary growth is initiated by the formation of primary cambium which arises from the parenchyma cells between the xylem and phloem groups except opposite to the two protoxylem groups where it arises from the pericycle. The cambium forms the innermost cambial ring (Fig. 11.25). It ceases to function after producing a ring

of closely arranged collateral vascular bundles (Fig. 11.25). The vascular bundles of the first ring are separated by comparatively narrow bands of radial parenchyma, which store food. After producing this ring of vascular bundles the primary cambium ceases to function. The second ring of cambium also called the first ring of secondary cambium arises from the phloem parenchyma (Artschwager, 1926) outside the first ring of primary cambium. The secondary cambial ring produces a second ring of secondary vascular bundles outside the first. The

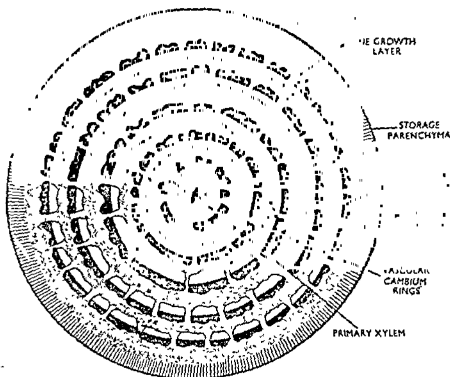


Fig. 11.25. *Beta vulgaris*. T.S. (diagrammatic) of storage root.

bundles are collateral (phloem and xylem in the same radius and phloem present only towards the outer border of xylem) and are separated by wide radial channels of secondary parenchyma which stores food material. This ring of cambium also ceases to function and a third ... of secondary cambium) is formed ... om the pericycle. Likewise, it also ... vascular bundles. The cells of the pericycle enclosed by the cambial ring undergo repeated divisions (proliferation) and form more pericyclic layers of parenchymatous cells. These cells also store food material. The subsequent cambial rings also develop from the pericycle and produce alternating layers of vascular bundles and **proliferated pericycle** (Figs. 11.25, 11.26), whose cells ...re food. The rings of pericycle appear dark-red and those of vascular

bundles are lighter in colour in a transverse section. The hypocotyl-cum root of *Beta vulgaris* increases in thickness by the activity of the concentric layers of cambium and by the proliferation of the pericycle.

Daucus Carota (*Umbelliferae*). Esau (1940) studied the developmental anatomy of the root of *Daucus carota* (Carrot). The secondary

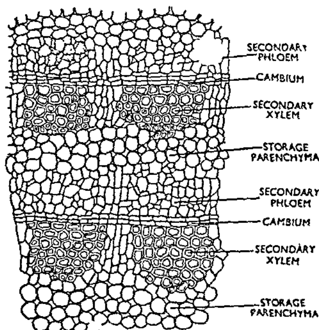


Fig. 11.26. *Beta vulgaris*. T.S. of a portion of storage root showing detailed internal structure.

growth in this case is normal and the only un-usual development is the formation of precocious amount of xylem and phloem parenchyma. Apart from the activity of the cambium, the proliferation of the parenchyma, which froms the storage tissue, adds to thickness of the root. Formation of supernumerary rings of cambia, as recorded for *Beta vulgaris*, has been reported for *Daucus*.

Ipomea Batatas (*Convolvulaceae*, Fig. 10.27). It exhibits a complicated anomalous secondary growth. Kamerling (1914), McCormic (1916) and Artschwager (1924) have described the anatomy of the tuberous roots of *Ipomea batatas* (Sweet potato). In the primary state the root is pentarch or hexarch. The cortex is wide with wide intercellular spaces. A well defined endodermis delimits the cortex from the stelar region.

To begin with the secodary growth is normal but at a later stage separate strands of secondary xylem and phloem are formed in the ground tissue. The xylem strands are later surrounded individually by

separate rings of secondary cambium (Fig. 11.27). The cambium arises from the parenchyma cells of the ground tissue surrounding the xylem vessels or groups of vessels.

The activity of the cambial cells surrounding the xylem groups leads to the formation of some secondary xylem elements towards the centre and a few sieve tubes and laticiferous elements away from the centre. Considerable amounts of storage parenchyma cells are formed in both directions. This storage parenchyma leads to the formation of tuberous root The larger vessels often become filled with **tyloses.**

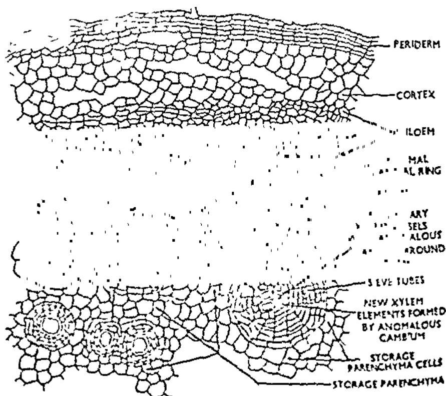


Fig. 11.27. *Ipomoea batatas*. T.S. portion of storage root showing detailed internal structure.

The cork cambium originates in the pericycle. The cortex of the mature root is mainly composed of secondary amyliferous tissue in which are embedded radial rows of sieve-tubes and some laticiferous elements.

An exactly similar type of anomalous secondary growth has been reported in *Convolvulus scammonia* by Dutailly.

Raphanus sativus (*Cruciferae*, Fig. 11.28). The fleshy roots of *R. sativus* (Radish) show a diarch primary xylem. The cambium appears

in a normal manner and cuts off secondary phloem towards the outside and secondary xylem towards its inner side. The secondary xylem contains a greater amount of xylem parenchyma. The cells of the parenchyma undergo considerable proliferation and increase in amount. Here and there, the cells of the proliferated parenchyma become meristematic and form cambia that partially or completely surround the groups of secondary xylem strands and by their activity produce more vascular and storage parenchyma. A transverse section of the mature fleshy root of *R. sativus* shows several distinct circular patches scattered in the ground tissue. These patches are composed of secondary cambial rings with a few vascular elements in the centre and large amounts of storage parenchyma cells formed internal as well as external to the cambial layer.

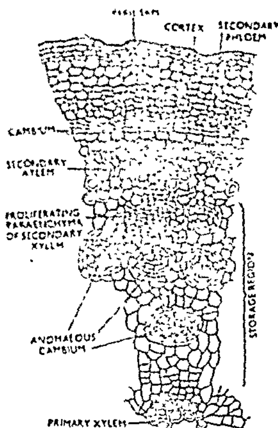


Fig. 11.28. *Raphanus sativus*. T.S. portion of storage root.

The original or the normal cambial ring is also recognisable in the peripheral region with sufficient amount of secondary phloem external to it.

EPIPHYTIC ROOTS

These are absorbing aerial roots that are usually found on the epiphytic orchids. The root of *Dendrobium* is taken here as an example to illustrate the structure of such a root. It is a monocot root and shows the following arrangement of tissue systems.

Velamen. [illegible] ter from the atmosphere. The water absorbed by these cells is later taken up by the living cells of the root.

Exodermis. It is a layer of thick-walled suberised cells and is made up of a single layer of cells (Fig. 11.29). A few thin-walled cells called the **passage cells** are present here and there in the exodermis.

The passage cells help in the passage of water from the velaman to the underlying cortex.

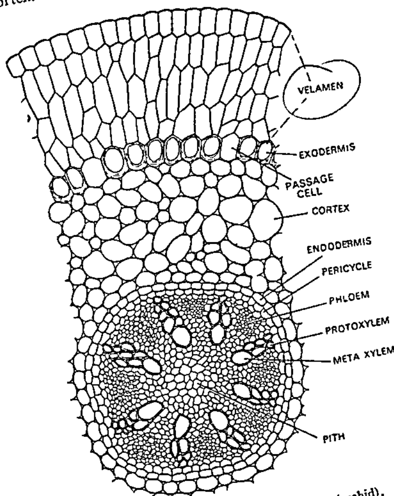


Fig. 11.29. T.S. aerial root of *Dendrobium* (orchid). Note the velamen and exodermis with passage cells.

Cortex. It is made up of several layers of parenchymatous cells that enclose small intercellular spaces. The outermost cortical cells contain chloroplasts.

Endodermis. It is the innermost layer of cortex and consists of barrel-shaped cells that contain starch grains. It completely encircles the stele.

Pericycle. It is composed of a single layer of thin walled-cells lying internal to the endodermis.

Vascular Region. It consists of six or more vascular bundles that are radial in organisation. The root is, therefore, polyarch.

Phloem bundles alternate with the xylem bundles. The xylem is exarch. The protoxylem consists of narrow vessels with annular and spiral thickenings on their walls. The metaxylem vessels are towards the pith and are larger in diameter with reticulate and pitted thickenings on their walls.

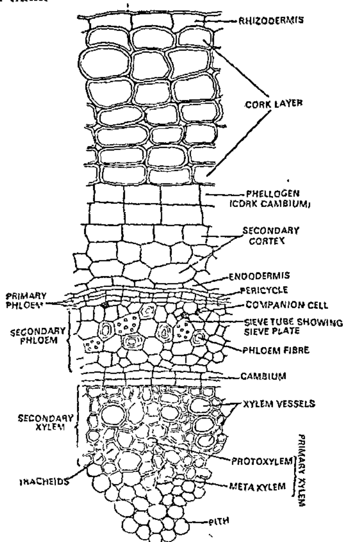


Fig. 11.30 T.S. [illegible]
sh [illegible]

The phloem lacks [illegible], companion cells and phloem [illegible].

The parenchymatous cells (mostly phloem and xylem parenchyma) around and in-between the xylem and phloem bundles constitute the conjunctive tissue.

Pith. There is distinct small (young root) or broad pith in the centre. Its cells are thin-walled and enclose small intercellular [illegible]

AERIAL ROOT OF BANYAN

Transverse section (Fig. 11.30) of *aerial* root of *Ficus benghalensis* reveals the following tissue systems from outside within.

Rhizodermis. It forms a single layer of almost rectangular cells. A layer of thick cuticle covers the rhizodermis.

Cork layers. There are many layers of cork cells that have suberised cell-walls and also enclose small intercellular spaces.

Phellogen. Next to the cork layers is the cork cambium or the **phellogen.** Its cells divide tangentially to cut off cork cells externally and secondary cortical cells internally.

The secondary cortex is composed of two or three or sometimes more layers of parenchymatous cells.

Endodermis and pericycle are also visible in young roots. The primary phloem is also recognisable and is almost crushed in roots that have undergone sufficient secondary growth.

The secondary phloem is quite distinct and has sieve-tubes, companion cells, phloem parenchyma and phloem fibres.

Next to the cambium, which forms a complete cylinder in older roots, is the xylem tissue. The primary xylem is recognisable towards the centre that is next to pith. The secondary xylem has tracheids, vessels and xylem fibres. Xylem parenchyma is scanty.

The pith is visible in young roots that have just undergone secondary growth. It becomes completely obliterated in older roots and is occupied by secondary xylem elements.

HETEROARCHIC ROOTS

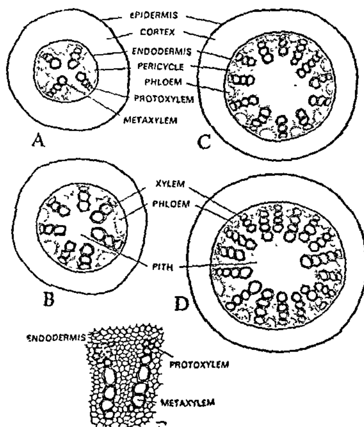
In dicotyledons the number of vascular bundles in the roots is limited and usually varies between 2—4 or in some cases five. Higher number has also been reported in exceptional cases. Majumdar (1932) reported as many as 12—14 xylem and phloem bundles in the aerial roots of *Vitis quadrangularis*. The number is usually constant in the roots of the same plant. There are some cases where a plant bears hetero-archic roots. It implies that a plant bears roots, some of which may be tetrarch, some pentarch, some hexarch and some polyarch. This condition is called **hetero-archy.** Wardlaw (1928) reported such a case in *Nymphaea chilensis* (*Gunnera chilensis*). This plant bears four kinds of roots :—

(i) Smaller roots that have 4 xylem groups (Fig. 11.31) alternating with 4 phloem groups (Tetrarch).

(ii) Slightly thicker roots that have seven xylem groups (Fig. 11.31) alternating with the same number of phloem groups.

(*iii*) Thicker roots with 12—14 xylem groups (Polyarch).

(*iv*) Thicker roots with 16—18 xylem groups (Fig. 11.31) (Polyarch).



All these roots lack secondary growth and arise on the same plant. They, however, vary in their diameter. Wardlaw (1921) reported **hetroarchic roots** in some species of *Eryngium* (umbelliferae). He found that in *Eryngium serra*, *E. pandanifolium*, and *E. bracteosum* the plants bear roots of different sizes. The smaller roots are tetrarch and the large roots may be hexarch, octarch or even polyarch: There is no secondary growth in the roots of these species.

Majumdar (1932, pp. 225—227) reported heteroarchic roots in *Enhydra fluctuans* (compositae). The terrestrial plants of this species bear tetrarch roots that have no pith and show secondary growth. Plants that grow along the banks of ponds possess two types of roots:—

(*i*) Thinner roots, that are triarch, possess pith and show no secondary growth.

(*ii*) Thicker roots that may be tetrarch or pentarch and may or may not possess pith and show little or no secondary growth.

Plants growing in water also possess two types of roots as described above. All these types of roots arise from the same node.

In *Cucurbita maxima*, the adventitious roots arising from the stem may possess 6, 7, 9, 11 xylem groups alternating with the same number of phloem groups. In *Lageneria*, the number varies between five to eight. In *Tropaeolum majus*, the main root is tetrarch whereas the adventitious roots are diarch. The lateral roots arising from the main tetrarch root are also diarch.

Heteroarchy was experimentally induced in *Pisum sativum* by Torrey (1955). He removed root tip segments measuring 500 μ from root apices of *Pisum sativum* and cultured them in sterile liquid media. After the excised tips resumed growth, Torrey found that 20% roots showed diarch or monarch xylem. Normally, the roots in this species are triarch. Torrey (1957) again treated the roots of the same species with IAA and found that, after resuming growth, the cultured roots became hexarch and remained so provided IAA concentration was maintained. In case the concentration was lowered the hexarch condition of xylem reverted to tetrarch or pentarch condition.

12

THE STEM

PRIMARY STRUCTURE

The stem is mainly concerned with reproduction and with the display of other [illegible]

ROOT-STEM TRANSITION

[illegible]

tion and the extent of the transition zone also vary. It may be present at the tip of the radicle, at the base or middle or at the top of the **hypocotyl**. The length of this region also varies from a little less than a millimetre to several centimetres. The time involved in these changes is also variable. The transition may be abrupt or gradual.

Eames and MacDaniels (1947, pp. 293—296 ; Fig. 134) have recognised 4 different types of transition in the various plants. These types (after Eames and MacDaniels) are discussed below :—

1. FUMARIA TYPE. In *Fumaria*, *Mirabilis*, and *Dipsacus* (Fig. 12.1, A), the primary xylem [illegible] divides radially into [illegible] the left and the other [illegible] rees and meet the phloem strands on their inner face. This method involves no change in the position of the phloem strand which passes as such into the stem. In this type the number of primary vascular

bundles, in the stem, corresponds to the number of phloem strands in the root.

2. CUCURBITA TYPE. In *Cucurbita, Tropaeolum, Phaseolus* and *Acer* (Fig. 12.1 B), there is a forking of both the xylem and phloem strands.

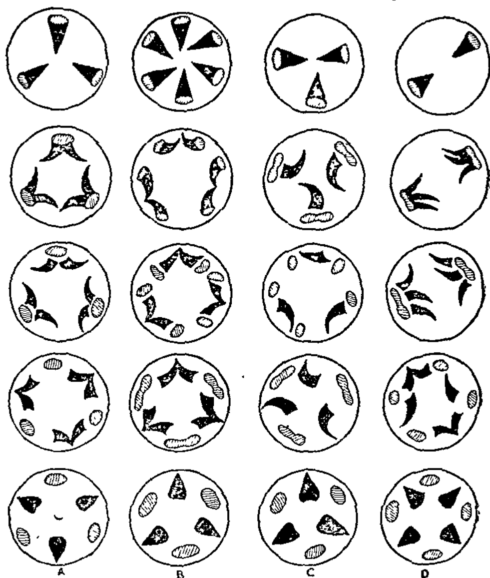


Fig. 12.1. Different types (A—D) of transitions in various plants. A, Fumaria type. B, Cucurbita type. C, Lathyrus type. D, Anemarrhena type. (*After Eames and MacDaniels*)

During their upward course the branches of each xylem strand turn laterally and become inverted *i.e.*, **excarch** position changes into the **endarch** position and join the inner face of the phloem strands. The phloem strands do not undergo orientation. In this type the number of vascular bundles formed in the stem is double (as compared to the

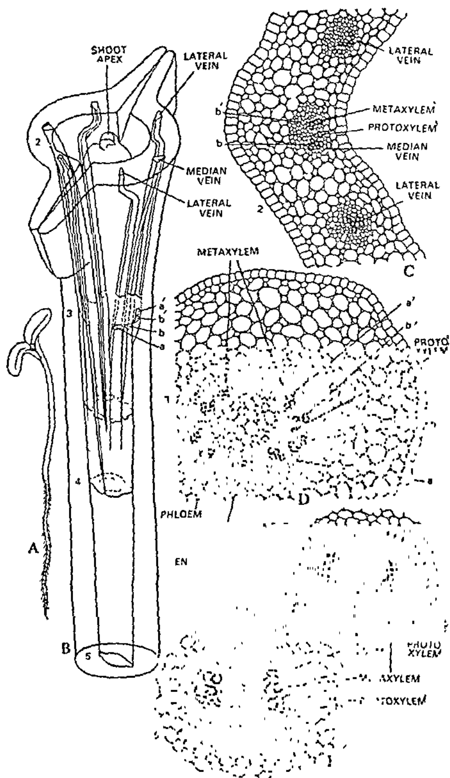


Fig. 12.2. It illustrates vascular transition in *Linum*. (*After Crooks, 1933*)

phloem strands in the root). If the root is triarch the number of vascular bundles in the stem will be six.

3. LATHYRUS TYPE. In *Lathyrus*, *Medicago*, and *Phoenix* (Fig. 12.1, C), the xylem strands do not undergo any splitting or forking but continue as such in the stem. They undergo a complete turning through 180 degrees so that the exarch position changes into endarch position. The phloem strands, in this case, divide and the branches come to lie in a position lateral to the xylem stands and meet the xylem strands at their outer faces. The divided phloem strands fuse again so that the number of vascular bundles remains the same as that of the phloem strands in the root.

4. ANEMARRHENA TYPE. In this type (Fig 12.1 D,) the stem possesses half the number of vascular bundles as there are phloem strands in the root *i e.*, if root is tetrarch the number of vascular bundles in the stem will be only two. Half of the xylem strands will undergo radial forking whereas the other half remain undivided. All the xylem strands become inverted and the branches of the forked strands turn laterally and join the undivided strands. The phloem strands do not divide but unite in pairs and fuse with the outer faces of the groups of the united xylem strands. So the vascular bundles in stem are reduced to half the number of phloem strands in the root and each vascular bundle is a composite structure made up of at least two phloem strands and a number of xylem strands. This type of transition is not common and is found only in a few monocots *e.g.*, *Anemarrhena*.

Vascular transition in Linum (Fig. 12.2). Crooks in 1933 described the root-stem transition in *Linum*. In this case the root is diarch. In the basal portion of the hypocotyl, the condition remains diarch but a little higher the hypocotyl shows the formation of the pith and splitting of the two phloem strands into four. A little higher the metaxylem starts developing on the sides of the two protoxylem groups leading to the formation of four groups of metaxylem. These metaxylem groups are in contact with inner face of the four phloem strands. This leads to the formation of four collateral vascular bundles. Each one of these collateral vascular bundles later on divides into two thus forming eight collateral vascular bundles. This happens somewhere in the middle of the hypocotyl. Higher up, these 8 bundles arrange themselves in two opposite groups of 4 each. The two vascular bundles flanking each group become separated from the central one and enter each cotyledon. They form the two lateral veins of the cotyledon. The two central vascular bundles in each group fuse with each other and enter each cotyledon as a median vein. The phloem strands of the root that divide into four in the hypocotyl form the [illegible] the first two leaves of the epicotyl. [illegible] bundles of these leaves develops [illegible] nent is basipetalous so that they ultimately join the strands of metaxylem in the hypocotyl or may end blindly in the parenchyma.

Vascular transition region in Helianthus annuus (Fig. 12.3). Daniel and Hilson (1973) studied the vascular transition zone in *Helianthus annuus*. Earlier, Siler (1933) and Thiel (1934) had described this zone in this species and found it to be unique in that there is an asymmetrical origin of the phloem in the intercotyledonary groups *i.e.*, the collateral bundles found in the plane separating the cotyledons. Daniel and Hilson (1973) found a bilateral differentiation of two types in this species besides the unilateral type. These will be described in brief here. The unilateral type is indicated as A-type and bilateral as B and B_1-types.

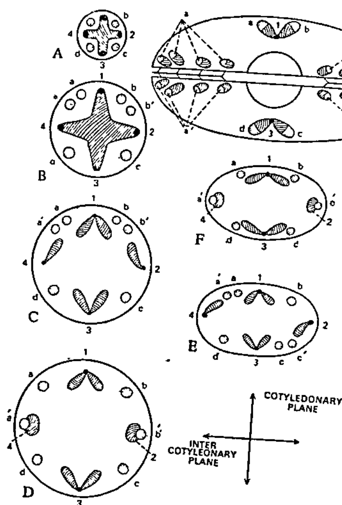


Fig 12.3. Vascular transition in H...

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Transition type-A (Unilateral Type)—It is illstrated in Fig. 12.3. The transition zone is located between 5·4 to 9·5 mm. from the root tip. Within this distance transition from root structure to stem structure is exhibited. In this case, out of four phloem groups only two groups lying on one side in the intercotyledonary plane divide; each into two phloem masses. The division of phloem bundles into two is brought about by the differentiation of several elongated pericyclic cells in the centre of each phloem group. The phloem groups in the figure are marked *a*, *b*, *c* and *d*. The phloem groups *a* and *b* divide into two masses *a'* and *b'* whereas *c* and *d* remain undivided. So now four masses of phloem are formed. These are *a'a b'b*. The xylem groups in the figure are labelled as 1, 2, 3 and 4. The newly formed phloem groups *a'* and *b'* develop laterally towards the protoxylem groups 4 and 2 respectively in the intercotyledonary plane. Simultaneously, the vascular cylinder enlarges and a definite pith develops in the centre in place of metaxylem elements which occupied the central area in the root. The new phloem groups develop towards xylem groups 4 and 2 where they assume a collateral position with these xylem groups. At the same time the xylem groups 1 and 3 in the cotyledonary plane bifurcate. As the phloem groups *a'* and *b'* differentiate laterally the xylem groups 4 and 2 (in the intercotyledonary plane) also develop laterally towards these phloem groups by the differentiation of metaxylem on the inner side of protoxylem. As the upper limit of transition zone is approached, the phloem groups *a'*, *b'* assume a collateral position with the xylem in the intercotyledonary plane forming two collateral bundles 4—*a'* and 2—*b'*.

The arrangement of the vascular tissue at the top of the transition zone, in the cotyledonary planes is more complex. The xylem bundles 1 and 3 lie in the cotyledonary plane and are flanked by phloem groups. The cotyledonary node lies about 8·7 mm. from the root tip and is marked by the formation of a furrow in the intercotyledonary plane. Ultimately, this node is marked by the appearance of two opposite clefts. These clefts mark the delimitation of the two cotyledons.

The two collateral bundles of the intercotyledonary plane bifurcate sharply and pass into each cotyledon, where they form the lateral bundles. These cotyledonary traces diverge into the cotyledon at right angles to the longitudinal axis of the hypocotyl. The lateral bundles bifurcate again to form several smaller bundles.

As the two double bundles of the cotyledonary plane diverge into the cotyledons, forming the median cotyledonary strands, the protoxylem occupies a deeper position in the axis than does the metaxylem. This orientation results in the endarch condition of the xylem. Higher up in the cotyledons the double bundles fuse forming a single bundle with endarch xylem.

Primary vasculature of the epicotyl differentiates basipetally until it forms a connection with the vascular system of the root-hypocotyledon unit.

Transition type-B (Bilateral Type) (Fig. 12.3)—In this case the phloem bundles *a* and *c* on opposite sides of the vascular cylinder divide into two new masses *a'* and *c'*. The new pholem groups *a'*, *c'* develop laterally towards protoxylem groups 4 and 2 in the intercotyledonary plane and form two collateral vascular bundles. In the meantime the xylem masses (1 and 3) in the cotyledonary plane bifurcate into two

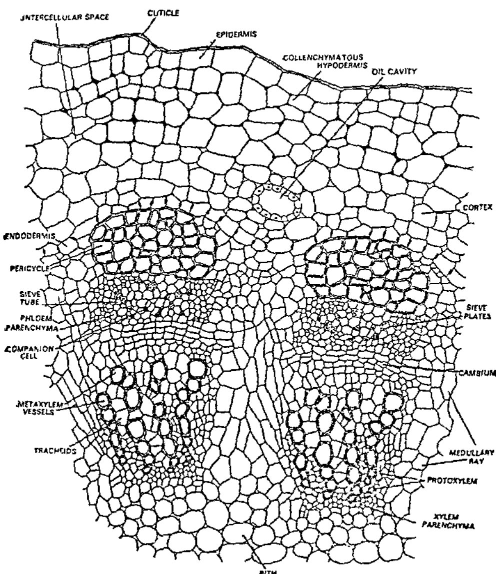


Fig. 12.4. T.S. Portion of stem of *Helianthus annuus* (*sunflower*, Dicot) showing detailed structure.

each. The arrangement of the vascular tissue in the hypocotyl and the vascularisation of the cotyledons follow the same pattern as in type A.

PRIMARY STRUCTURE OF A DICOTYLEDONOUS STEM

Internal structure of a dicotyledonous stem reveals the existence of three tissue systems ; the **dermal** or **epidermal tissue system**, the **fundamental** or the **ground tissue system** and the **vascular** or **fascicular tissue system.**

The dermal or the epidermal tissue system is generally composed of a single layer of cells, called the **epidermis** and differentiates from the surface layer of the shoot apical meristem *i,e.,* the outermost layer of tunica in the angiosperms.

Epidermis. It is protective in function and forms the outermost layer of the stem. It is generally made up of a single layer of cells, which appear almost rectangular in a transverse section. The cells are compactly arranged and do not possess intercellular spaces. The cells are living and are capable of mitotic division in a radial plane and undergo tangential enlargement. This characteristic of the

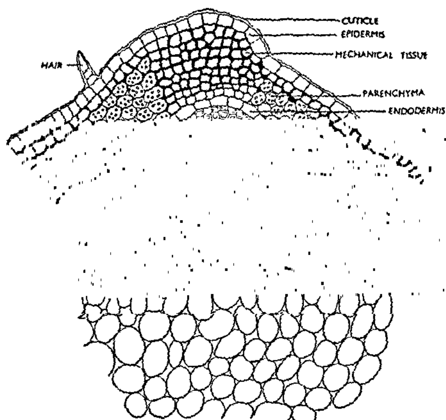


Fig. 12.5. T.S. through a portion of stem of *Medicago sativa* showing detailed primary structure.

epidermal cells enables this layer to withstand the stresses to which it is subjected by primary and secondary growths of the stem. In *Viscum*

album and *Acer striatum*, the epidermis through continual radial division remains as a relatively permanent layer. A forty-year old trunk of *Acer striatum* is sometimes covered by true epidermis. The outer walls of the epidermal cells are highly cutinised, while waxy coats and hairy covering occur in many cases. Presence of cuticle and other waxy substances makes it almost a waterproof layer so that very little water is lost by transpiration. Hair which are outgrowths of epidermal cells may be present sparingly or in such numbers in certain plants as to give the stem a woolly appearance. Stomata are present to a limited extent in the epidermis of the stems.

Cortex. Next to the epidermis is a few to several-layered thick zone of cells, called the **cortex.** This region can be distinguished into two zones in stems like Sun-flower (Fig. 12.4), *Medicago sativa* [illegible] *ita* (Fig. 12.12). One of these [illegible] made up of varying layers [illegible] ie epidermis. In *Medicago sativa* and *Cucurbita* stems, the hypodermis is well developed (Figs. 12·5 and 12.12) beneath the ridges and is single-layered or absent elsewhere. In *Ricinus communis*, the collenchyma forms a continuous layer below the epidermis and is 1—5 layers thick (Fig. 12.6 and 12.7). The cells have localised thickenings and may possess chloroplasts. So this layer serves a dual function of protection and photosynthesis. In many dicots *e.g.* *Ranunculus*, *Fumaria* etc., collenchymatous hypodermis is absent (Fig. 12.10) and the entire

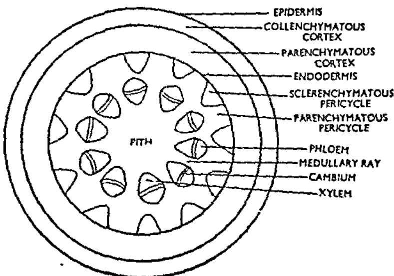


Fig. 12.6 *Ricinus communis*. Outline sketch of a T.S. through young stem showing primary structure

cortex is parenchymatous. Next to the hypodermis is the general **cortex** or the median part of the cortex. It consists of a few layers of loosely packed parenchymatous cells most of which contain chloroplasts. There are prominent intercellular spaces in this part

of the cortex. The cells are generally large, rounded, oval and, sometimes, polygonal. In sun-flower stem, isolated resin ducts lined with secretory cells are seen in this part of the cortex. In *Ricinus*

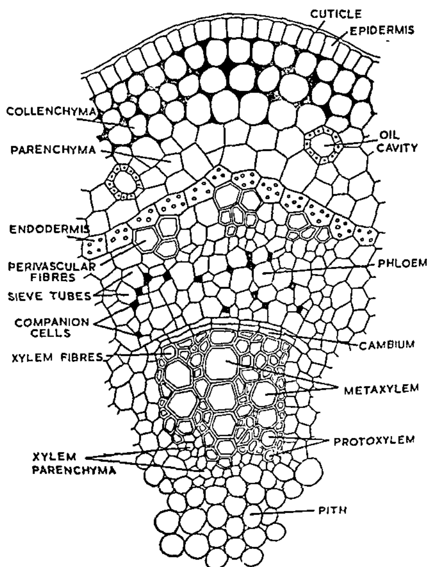


Fig. 12.7. T.S. through portion of stem of *Ricinus communis* (dicot) showing detailed internal structure.

communis (castor oil) the cortex contains a number of oil cavities (Fig. 12.7). Presence of sclereids has also been reported in the cortex *e.g.*, *Nuphar*, *Euryale*. *Nymphaea*, etc. Laticifers are also present in the cortex of many stems *e.g. Euphorbia splendens*. Large air spaces or *lacunae* are present in the cortex of stems of some water plants *e.g. Nuphar*, *Euryale*, *Nelumbo*, *Cabomba* etc.

The innermost layer of the cortex which delimits it from the stele is called the **endodermis**.The cells of the endodermis are usually barrel-

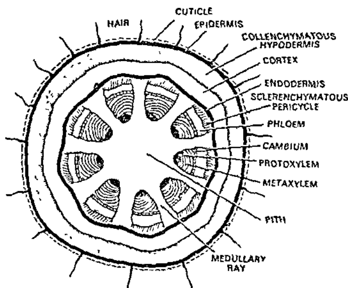


Fig. 12.8. T.S. stem *Xanthium* (diagrammatic).

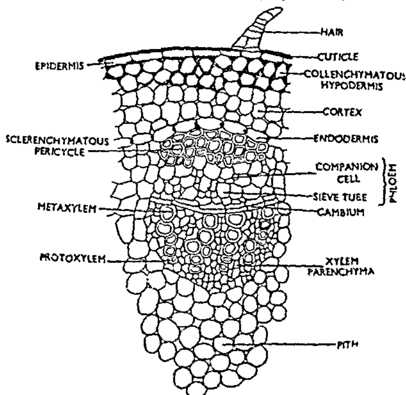


Fig. 12.9. *Xanthium* T.S. through a portion of stem, showing detailed internal structure.

shaped and accumulate starch. It is, therefore, recognised as a starch-sheath. Majority of the dicots and the conifers lack a morphologically differentiated endodermis It is impossible or difficult to delimit cortex from the vascular region, if the intermost layer of the former lacks

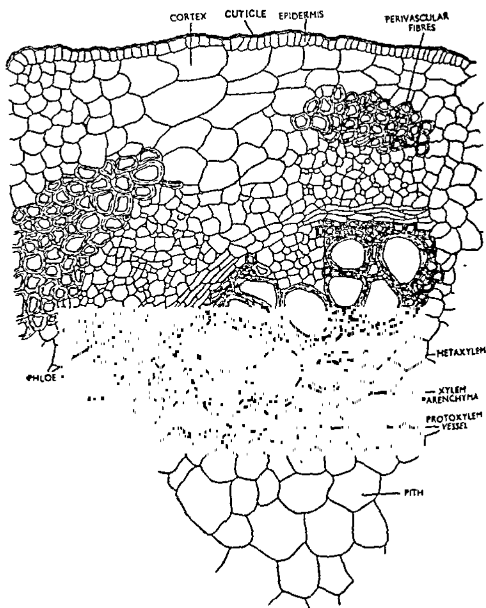


Fig. 12.10. *Fumaria.* T.S. Portion of stem showing detailed internal structure.

starch and the casparian bands. Van Fleet (1950) has demonstrated the occurrence of certain chemical reactions between the materials derived from the vascular region and cortical region in the innermost

layer of the cortex. Ziegenspeck (1952) has pointed out that these reactions are similar to those that take place in the endodermis. These observations clearly indicate that there is certainly a physiological delimitation between the vascular regions and cortical regions of the stem. It may or may not be accompanied by a morphological differentiation. Esau (1960) used the term endodermis only when innermost layer of cortical cells possesses casparian strips or bands. She uses the term **endodermoid layer** for a layer in similar position and showing physiological differentiation from adjacent layers. The endodermoid layer lacks casparian bands.

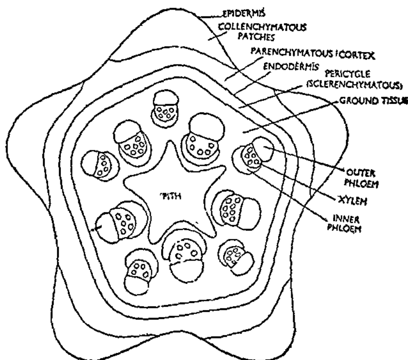


Fig. 12.11. Diagrammatic cross-section through *Cucurbita* stem. Note the presence of ten vascular bundles (bicollateral) arranged in two rings, hollow pith, and continuous cylinder of sclerenchymatous pericycle.

Pericycle. The term pericycle is given to a layer or layers of cells that occur between the endodermis and the vascular cylinder. In ... Fig. 12.12), the pericycle occurs ... the vascular region. In *Helian-* ... *a* it forms alternating patches of ... The thick-walled patches occur above the phloem and have also been called **hardbast.** The thin-walled patches are above the medullary rays and are scarcely distinguishable from the cells of the rays. In *Cucurbita* and some other members of the family *Cucurbitaceae*, the sclerenchymatous pericycle occurs in the form of a continuous cylinder made up of several layers of cells (Fig. 12.12). The same is the case with *Aristolochia* and *Cassia*. In *Pelargonium*, the

pericycle originates from the same meristem as the phloem. In *Aristolochia* and *Cucurbita* it originates outside the phloem (Blyth, 1958) and is thus non-phloic in origin. Esau (1960) designates this layer as **primary phloem fibres** if its origin is phloic and **perivascular fibres** if its origin is non-phloic. She uses the term **primary extraxylary fibres** for both the kinds of fibres.

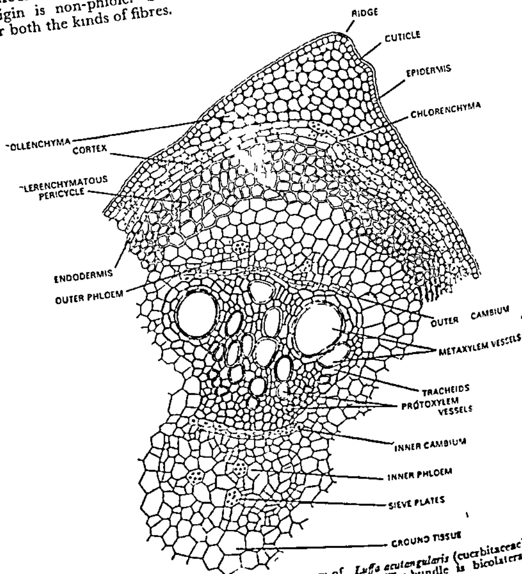


Fig. 12.12. T.S. through a portion of the stem of *Luffa acutangularis* (cucrbitaceae) showing detailed structure of one vascular bundle. The bundle is bicolateral and has both outer and inner cambial strips.

The sclerenchymatous patches of pericycle in sun-flower and *Medicago sativa* are made up of long needle-shaped cells with much thickened walls. With maturity the walls increase in thickness and become rigid, thus aiding to support the stem.

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food and water at any level in the stem.

Pith ... sue and is exten-
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... thus distinguish-
ing peripheral portion of the pith from the central part. In many stems the pith may be absent in the internodal areas and present only in the nodal region (as nodal diaphragm). Pith cells may also contain chloroplasts *e.g., Lantana, Lonicera flava.* Laticifers, sclereids, idioblasts, crystals of various types and other ergastic substances are also found in the pith.

Vascular System. The primary vascular tissues differentiate from the procambium, which in turn develops from the derivatives of the apical meristem. The vascular system encircles the pith and usually occurs as a cylinder between the cortex and pith. It may assume complicated patterns in some cases. In majority of the dicots *e.g.,* ... e vascular cylinder
... **vascular bundles**
... *and Phlox* it appears
to be a continuous cylinder but closer examination reveals that in this case the vascular bundles are too close to each other and the interfascicular regions are extremely narrow. Same is the case in *Lonicera.*

In the dicot stems the vascular bundles are discrete and arranged in the form of a ring (Figs. 12.3, 12,4 and 12.5). Each vascular bundle is composed of two types of vascular tissues : (1) the **phloem,** and (2) the **xylem.** In-between these two vascular tissues is a strip of meristematic cells, the **vascular cambium.** The arrangement of the phloem and the xylem is **collateral** as seen in a cross-section, with phloem towards the outer side and xylem towards the pith. Presence of **cambium** makes the bundles **open.**

In the families *Apocynaceae, Asclepiadaceae, Convolvulaceae, Cucurbitaceae, Solanaceae,* and certain members of the *Compositae,* the phloem is present on either side of the xylem (Figs. 12.11, 12.12 and 12.14). Such vascular bundles which have phloem on two sides of the xylem are called **bicollateral bundles.**

In *Begonia, Mesembryanthemum crystalinum* and *Rumex,* the medulary bundles are **amphivasal** (xylem surrounds the phloem). In *Phlox,* the vascular cyclinder is continuous and consists of a single-layered pe ... id
a ... is
ar ...

The *Nymphaeaceae* show interesting examples of polystele. In *Victoria amazonica,* the thick rhizome has many steles, each stele

possesses a ring of about 20 vascular bundles. In the rhizome of *Nymphaea mexicana*, there are 4 or 8 steles each having its own endodermis. In *Cab mba* there are only two steles each having two vascular bundles. True vessels are absent in this family. Tracheids are long and spiral or annular. The bundles are closed *i.e.*, cambium is lacking. The xylem fibres are also absent.

Phloem A detailed description of primary phloem has already been given in chapter five. This tissue lies next to pericycle. In sunflower stem, it is immediately below the sclerenchymatous patches of pericycle (Fig 12.4). It is composed of four types of cells : (*i*) **sieve-tubes**, (*ii*) **companion cells**, (*iii*) **phloem parenchyma**, (*iv*) **phloem fibres**. The sieve-tubes are thin-walled elongated cells that are placed one above the other forming long pipes (Fig. 12.13) for the conduction of food materials. Their cross-walls are perforated like a sieve. Such cross-walls, which are a characteristic feature of the sieve-tubes, are

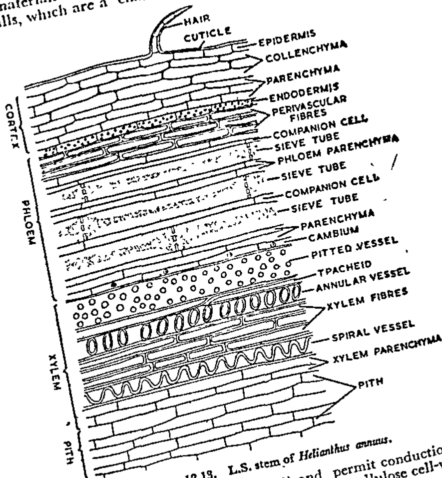


Fig. 12.13. L.S. stem of *Helianthus annuus*.

called the **sieve-plates** (Fig. 12.13) and permit conduction of food material. The sieve-tube cells have a thin cellulose cell-wall with a

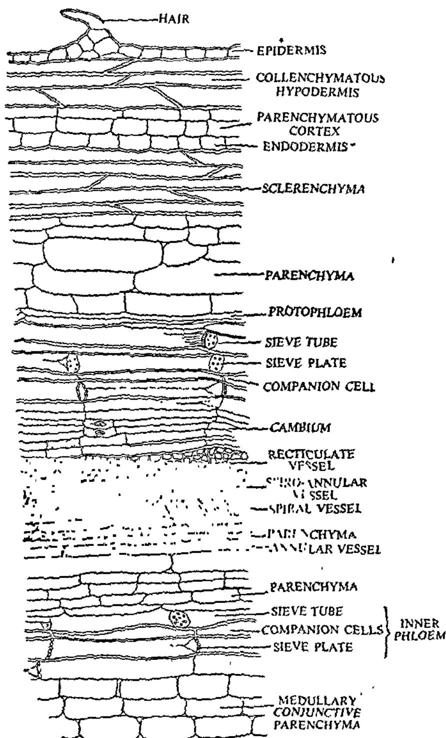


Fig. 12.14. Longitudinal section through portion of the stem of *Cucurbita*.

lining layer of peripheral cytoplasm and a big central vacuole. The nucleus is absent. The vacuole is filled with a proteinaceous slimy fluid. The **companion cells** are small parenchymatous cells that are associated with the sieve-tubes (Fig. 12.13). They have thin cellulose cell-wall and cytoplasm possesses a distinct nucleus. In a transverse section the sieve-tube appears as a bigger polygonal cell. The function of the companion cells is obscure. Major portion of the phloem is made up of living parenchyma cells, which occur in abundance and store food-material in the form of starch, *protein, and fats*. In non-functional phloem, the phloem parenchyma cells become lignified and change into phloem fibres *e.g., Ranunculus, Fumaria* (Fig. 12.10) etc. *In some dicots like Nerium* the phloem fibres occur outside the phloem *i.e*, next to the pericycle. [illegible] hs and their walls have both cellulose [illegible] ells and may be formed as a result [illegible] when it is disorganised.

Cambium. It is a thin strip of cells extending length-wise between xylem and *phloem* (Fig. 12.14). *It consists of a single layer of* meristematic cells which appear almost rectangular in a transverse section, and have thin walls (Fig. 12.12). The division of cambial cells adds to the phloem and xylem and is responsible for growth in thickness (secondary growth). The cambium is absent in the vascular bundles of many *Nymphaeaceae* (*Nymphaea Nelumbo* etc).

Xylem Maturation of primary xylem cells starts at the inner face of each provascular strand and progresses outwards. The xylem of a [illegible]
or [illegible]
(4) [illegible]
cells placed one above the other with their cross-walls dissolved thus forming long pipes that aid in conduction of water and mineral substances dissolved in it. They are dead cells with lignified secondary walls. The thickening material is laid down in the form of **spirals** and **rings** (annular in the vessel found towards the pith). They are narrower and older and constitute the first formed xylem elements or the **protoxylem.** The xylem vessels found near the cambial strip and middle have **pitted, scalariform** and **reticulate** thickenings and constitute **metaxylem** or the later-formed xylem. The vessels of the metaxylem are broader. Such arrangement of vessels in which the protoxylem is towards the centre and metaxylem towards the outside is called **endarch.**

The metaxylem is surrounded by long thick-walled and narrow cells, called the **tracheids.** They are elongated cells that taper at their ends and are lying one above the other. Sometimes, their cross-walls get dissolved and they help in conduction. Generally, their function is to give mechanical strength to the stem. In transverse section they appear polygonal or rounded in shape.

The xylem fibres or the wood fibres are also elongated cells with tapering ends and have very thick walls. They are dead cells and give mechanical strength to the organs.

The wood parenchyma cells are living and make up the ground mass of the xylem tissue. It makes up large proportion of the primary xylem. Their walls are made up of cellulose. They store food-material.

The vascular bundle of a dicot stem like sun-flower can be described as **conjoint** (because it consists of both xylem and phloem), **collateral** ... same radius and phloem ... **open** (because cambium is ... **endarch** ... found towards the inner face next to the pith).

PRIMARY STRUCTURE OF STEM IN CUCURBITACEAE

Ekendranath Ghosh (1932, 259—270) studied the primary structure of the stems of 14 species belonging to nine genera of the family *Cucurbitaceae*. The stems in majority of the *Cucurbitaceae* are ribbed and may be radially symmetrical in transverse section (*Benincasa cerifera, Trichosanthes palmata*, etc.) or bilaterally symmetrical (*Coccinia indica*). The ridges are sharp and raised in all the species of *Luffa* and in *Trichosanthes palmata*. The ridges are depressed in *Citrulus vulgaris*. Majority of the species have rounded ridges *e.g., Cucurbita pepo, Cucumis melo, C. sativa. Lagenaria vulgaris* and others.

Epidermis. It is made up of a single layer of compactly arranged cells. The cell-shape varies with species. They are cubical in *Benincasa cerifera, Lagenaria vulgaris* and *Trichosanthes palmata* , oval in all the species of *Luffa, Momordica cochinchinensis, Coccinia indica*, and *Trichosanthes dioica* ; elongated in *Trichosanthes anguina*. In *Cucumis melo, C. sativa, Cucurbita pepo* and *Momodica charantia*, the epidermis is made up of oval and ...
contour of the epiderm ...
Coccinia indica and ...
hair. The multicellular hair may have a single basal cell or they may be seated on a multicellular base (*Cucurbita pepo*). Glandular hair are ...

4 cells.

Cortex. The cortex is distinguishable into two clearly defined regions. The outer cortex or sometimes called the **hypodermis is collenchymatous.** The collenchymatous cortex is made up of variable number of cell layers. It is usually well-developed below the ridges. It forms a continuous band of collenchyma in *Coccinia indica, Cucumis*, and *Trichosanthes*. It occurs in isolated paches in a number of species ... the ridges. In *Cucurbita* ... the ridges and may be ... ws. In species with a continuous ring of collenchyma, it is well-developed below the ridges, whereas below the grooves the collenchyma layers are comparatively fewer in number. Collenchyma is completely wanting in *Momordica*

cochinchinensis. The collenchyma cells usually contain chloroplasts. Next to collenchyma is the parenchymatous cortex which consists of ordinary thin-walled cells arranged in variable number of layers. The layers vary from 1—14 The number of parenchyma layers is more below the ridges and less below the grooves or furrows. In *Cucurbita*

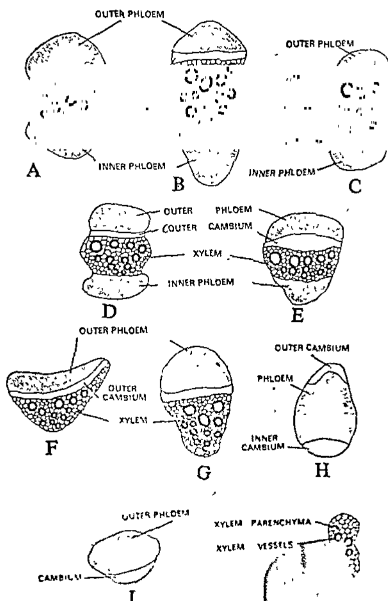


Fig. 12.15. (A—J). Types of vascular bun- Cucurbitaceae.
A. Complete ridge bundle of *Citrulus*
B. Complete ... of *Cucumis* ...
C. Comple... of *Coccinia* ...

pepo, there are 6—7 layers of parenchyma below the ridges and 4—5 layers below the furrows. In *Luffa acutangularis* there are 9—10 layers below the ridges and 1—5 below the furrows. In *Luffa aegyptiaca* the number varies from 12—14 below the ridge and 1—3 below the furrows.

Endodermis. It is made up of a single layer of uniform cells. The cells are generally smaller than those of the cortex. In *Momordica cochinchinensis*, the endodermis is composed of irregularly arranged cells of unequal size.

Pericycle. It is made up of several layers of sclerenchymatous cells and is very distinct in the cucurbit stems. The general outline of the pericycle may be circular (*Coccinia indica*) or sinuous (*Cucurbita, Luffa, Lagenaria,* etc.). It may be of uniform thickness throughout its contour or its thickness may vary In the latter case the number of layers is more below the ridges.

Vascular Bundles. There are generally two rings of vascular bundles. The outer ring of usually smaller bundles is present below the ridges and may be designated as **ridge bundles.** The inner ring of larger bundles is usually present below the furrows and may be called as **furrow bundles.**

(*a*) **Ridge Bundles.** They are usually five in number. In *Trichosanthes palmata*, there are 7 ridge bundles. The ridge bundles may be :—

(*i*) **Complete.** The complete bundles have an outer phloem, outer cambium, xylem, inner cambium, and inner phloem (Fig. 12.15, A—C). Such bundles are present in *Coccinia indica, Cucumis melo, C. sativa, Luffa aegyptiaca, L. acutangularis, Momordica cochinchinensis* and *Cucurbita pepo.*

(*ii*) **Incomplete.** These bundles do not possess inner cambium *e.g., Lagenaria vulgaris, Trichosanthes, Momordica charantia, Benincasa cerifera,* and *Citrullus vulgaris.*

The ridge bundles are usually of equal size except in *Coccinea indica* where they are unequal in sizes. The shape of these hundles is usually oval or nearly rounded. They may be elongated and narrow in *Cucumis melo.* These elongated bundles are bilobed in *Coccinia indica, Cucurbita pepo, Momordica charantia, Cucumis sativa,* and *Trichosanthes dioica.* In *Benincasa cerifera* and *Trichosanthes anguina* the bundles are elongated and trilobed.

→ D. Incomplete ridge bundle of *Benincasa. cerifera* There is no inner cambium.
E. Incomplete furrow bundle of *Trichosanthes anguina.* Inner cambium is absent.
F. Incomplete and collateral bundle of *Trichosanthes anguina.* Inner cambium and inner Phloem are absent.
G. Incomplete collateral furrow bundle of *Lagenaria vulgaris.*
H. Incomplete furrow bundle of *Lagenaria vulgaris.* There is no xylem.
I. Incomplete furrow bundle of *Trichosanthes dioica.* Outer phloem, outer cambium and xylem are absent.
J. Xylem bundle below the furrow in *Momordica charantia.*

(All after Ghosh, 1932)

The shape of the phloem tissues also varies in various species. The outer phloem may be flattened, band-like and curved (*Cucurbita pepo, Luffa aegyptiaca*), crescentic (*Luffa acutangularis*), planoconvex (*Cucumis melo, C. cochinchinensis*) and biconvex ((*Trichosanthes anguina*). The inner phloem may also be flattened, band-like and curved (*Trichosanthes*), crescentic (*Citrullus vulgaris*), triangular (*Lagenaria vulgaris*) and semicircular (*Trichosanthes anguina*).

The outer cambium is generally flattened or band-like. The inner cambium is usually in the form of a curved band. In *Coccinia indica* both the outer and the inner cambia are curved and band-like.

The xylem is sandwiched between the phloem patches and is well developed It is in the form of a broad or a narrow band. The metaxylem vessels are usually towards the outer phloem and protoxylem towards the inner phloem. The xylem is, therefore, typically endarch. The vessels are normally rounded or oval in shape.

(*b*) **Furrow Bundles**. The number of furrow bundles may be the same as ridge bundles or it may be more or less than the ridge bundles. The ridge bundles are usually 5—7 in number whereas the furrow bundles vary in number from three to eight. The furrow bundles are usually larger in size than the ridge bundles. They may all be of equal size

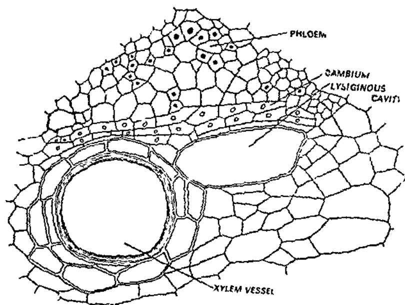


Fig: 12.16. An incomplete vascular bundle of *Luffa acutangularis*. It has no inner phloem and inner cambium

or their sizes may vary in the same ring. Their shapes may be oval wedge-shaped and elongated, and may be single or lobed. Like the ridge bundles the furrow bundles may be complete (*Momordica cochinchinensis, Trichosanthes, Cucumis, Cucurbita pepo, Lagenaria vulgaris, Luffa*) or incomplete (without inner cambium). In *Lagenaria vulgaris*

the inner ring of the furrow bundles includes two medium-sized vascular bundles that have no xylem and possess only outer pholem, cambium and inner pholem. In the same species there is one furrow bundle that is collateral *i.e.*, it lacks inner cambium and inner phloem. This bundle is the smallest in the ring. *Lagenaria vulgaris* also possesses one small furrow bundle that has phloem in the middle, bordered on outer and inner faces by a strip of cambium (Fig. 12.15, H.) In *Trichosanthes dioica* the furrow bundles include one bundle with only outer pholem and a cambium (Fig. 12.15. J). In *Momordica charantia* one of the small fnrrow bundles is made up of xylem only. It has xylem vessels and tracheids bordered by xylem parenchyma on the outer and inner faces (Fig. 12.15, J.) In *Trichosanthes anguina* some of the furrow bundles have only outer phoelm, outer cambium and xylem (Fig. 12.15, F). Some rudimentary furrow bundles have also been recorded in *Momordica charantia*. These bundles consist of a patch of undifferentiated cells only.

Pith It is made up of thin-walled cells which enclose small and large intercellular spaces. In some species, the pith is hollow. The hollow pith cavity may be large and round (*Benincasa cerifera*), large and irregular (*Cucurbita pepo, Cucumis melo* and *Coccinia indica*), small (*Lagenaria vulgaris, Trichosanthes*) and triradiate (*Luffa acutangularis*).

T.S. Stem of Luffa acutangularis. A transverse section of a young stem of *Luffa acutanglaris* presents an irregular outline with usually five ridges and five furrows It consists of the following tissues (Fig. 12.12) :—

Epidermis. It forms the outermost layer of stem and consists of a single row of compactly arranged thin-walled cells The epidermis is covered with a cuticle. It also bears numerous multicellular hair. It is a protective layer.

Cortex. It is distinguished into three regions : (*i*) **Hypodermis,** (*ii*) **Chlorenchymatous cortex,** (*iii*) **Endodermis.**

The hypodermis [illegible] ped below the ridgès and [illegible] cells. Below the grooves [illegible] only of one or two layers. The cells contain chloroplasts. This tissue, in this case, performs dual function of photosynthesis and mechanical support.

The general cortex is made up of two or three layers of thin-walled cells that contain abundant chloroplasts. Below the furrows it extends upwards right up to the epidermis. The cells store food and also are a seat of photosynthesis.

The **endodermis** forms the innermost layer of cortex and consists of a single layer of thin-walled barrel-shaped cells. The cells contain starch grains.

Pericycle. It forms a continuous zone of thick-walled cells arranged in four or five layers. The cells appear polygonal in outline in a cross-section and have thick and lignified walls. They do not possess cytoplasmic contents. It gives mechanical strength to the stem.

Ground Tissue. The stem is hollow and does not possess pith. The continuous parenchymatous mass of cells, next to the pericycle with vascular bundles embedded in it, constitutes the **ground tissue**. The cells have thin walls. Immediately below the pericycle the cells are smaller in size, polygonal, and compactly arranged. Towards the centre the cells are larger in size, rounded and possess intercellular spaces

Vascular System It is composed of ten vascular bundles arranged in two rings. Five in the outer ring are smaller in size and are present below the ridges. Five in the inner ring are large in size and are found below the furrows The vascular bundles are **conjoint, bicollateral, open** and **endarch**. Each vascular bundle consists of: (1) **Outer phloem,** (2) **Outer cambium,** (3) **Xylem,** (4) **Inner cambium** and (5) **Inner phloem.**

Phloem It occurs in the form of outer and inner patches on either side of the xylem (Fig 12.12). The outer patch appears planoconvex and the inner semi-lunar in a transverse section (Fig. 12.12). It consists of the usual cell types *i.e.*, the sieve tubes which are very prominent, the companion cells, and the phloem parenchyma which makes up most of the tissue. The sieve plates are also distinctly seen.

Cambium. It forms two strips of thin-walled meristematic cells, one each towards the outer and the inner border of xylem, thus making the bundle open. The cells are more or less rectangular in shape. The cambial strip between the inner phloem and xylem is curved.

Xylem. It is sandwiched between the outer and the inner patches of phloem It consists of wood vesselss, tracheids and wood parenchyma The vessels are scattered and not arranged in radial rows. The vessels towards the inner side are narrow with annular, spiral and reticulate thickenings (Fig. 12.12). They constitute the protoxylem. The vessels towards the outer side are wide with pitted thickenings and constitute metaxylem. Tracheids and wood fibres are also present, but in smaller numbers. Wood parenchyma is abundant.

Phylloclade of Ruscus. It is a modification of the stem. In this case a branch becomes flattened like a leaf and assumes a dorsiventral symmetry. A transverse section (Figs. 12.17 and 12.18) reveals the following structures :—

Epidermis. Both the upper and the lower layers of epidermis are made up of a single layer of cells that are arranged compactly and are covered by cuticle. The continuity of the epidermal layers is broken by the presence of stomata.

Chlorenchyma. It is sub-epidermal and is represented by one or two layers of loosely arranged parenchymatous cells below the upper epidermis. The cells contain many chloroplasts.

Next to the chlorenchyma is the parenchymatous region. It is composed of several layers of thin-walled loosely, arranged cells. It extends between the chlorenchyma and the lower epidermis.

Vascular System In the centre there is a well-developed vascular region or the stele. It consists of a sclerenchymatous sheath surrounding a number of amphivasal vascular bundles that are scattered. Each bundle consists of phloem surrounded completely by xylem. The rest of the bundles are small and amphivasal (phloem in the centre and xylem surrounding it). The vascular elements are well-developed and distinct.

The leafy characteristics of the phylloclade are : (*i*) dorsiventral symmetry with upper and lower epidermises ; (*ii*) flattened and leaf-like structure ; (*iii*) presence of chlorenchyma , and (*iv*) presence of

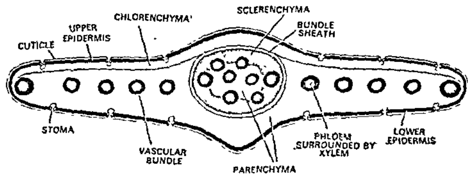


Fig. 12.17. T.S. phylloclade of *Ruscus* (diagrammatic)

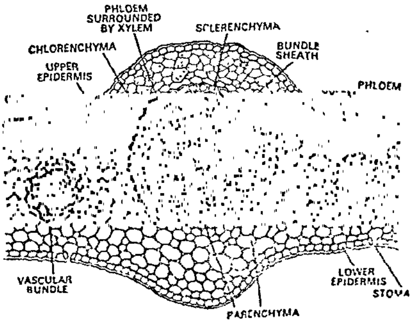


Fig. 12.18. V.S. Portion in detail of phylloclade of *Ruscus*. Vascular bundles in the mid-rib are scattered and are **amphivasal.**

stomata. The stem characteristics are : (*i*) presence of amphivasal vascular bundles ; (*ii*) phloem does not face the lower epidermis *i.e.*, the bundles lack orientation characteristic of the leaves ; and

(*iii*) presence of distinct parenchyma (comparable to ground tissue or pith) in the central stele.

Phylloclade of Coccoloba platyclada (Fig. 12.19). A transverse section of the dorsiventrally flattened phylloclade of *Coccoloba platyclada* (=*Muehlenbeckia platyclada*) shows the following tissues :—

1. **Epidermis.** It is covered by a thick cuticle and consists of closely packed rectangular cells. Many sunken stomata interrupt its continuity.

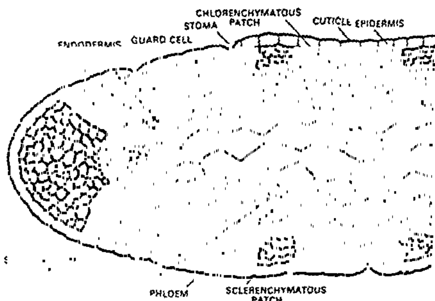


Fig. 12 19. T.S. Phylloclade of *Coccoloba platyclada*.

2. **Hypodermis** It consists of numerous and discrete sclerenchymatous patches. Sclerenchyma is well-developed at the corners of the flattened phylloclade and give it mechanical support.

3. **Palisade tissue.** It occurs in the form of patches of chlorenchymatous cells that alternate with the sclerenchymatous patches. The cells contain many chloroplasts. They constitute the cortex. One or more layers of nonchlorophyllous cells may also be present below the palisade and sclerenchyma patches.

4. **Endodermis** It forms an irregular layer of barrel-shaped cells that are devoid of casparian strips but contain starch grains.

5. **Pericycle.** It is made up of a single layer of rounded or oval cells next to the epidermal layer.

6. **Vascular Region.** It consists of numerous discrete bundles that lie beneath the sclerenchymatous patches of hypodermis. The [illegible] The bundles form [illegible] and xylem [illegible] loem fibres. Phloem parenchyma is scanty. Xylem has tracheids, vessels and little parenchyma. Fibres are absent in the xylem.

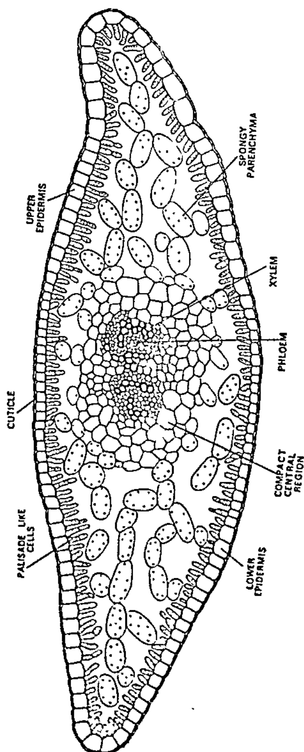
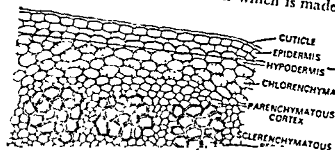
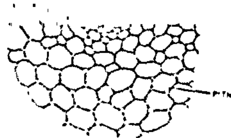


Fig. 12.20. T.S. Phylloclade of *Asparagus*

7. **Pith.** A distinct parenchymatous pith is present in the centre. The cells enclose intercellular spaces.

Stem of Salvadora. It is an exmple of an anomalous dicot stem possessing interxylary or included phloem (Fig. 12.21). A transverse section of the stem reveals a single-layered epidermis followed by a two-layered hypodermis of thin-walled cells. After the hypodermis is a 2 –5-layered chlorenchymatous cortex which is made up of almost





single layer of brick-shaped cells but appears many-layered due to slow development of the cells cut off by it, into secondary vascular

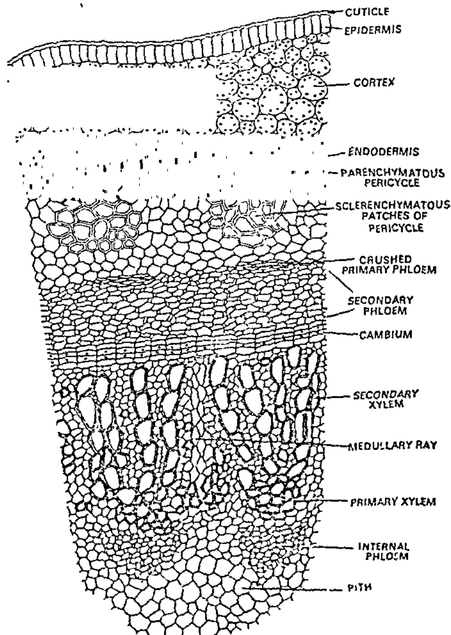


Fig. 12.22. T.S. stem of *Calotropis procera*. Note the groups of internal phloem.

elements. The interxylary or included phloem develops centripetally. The incuded or interxylary phloem develops in distinct patches due to *irregular activity of the cambium ring. Certain cells of the cambium* which normally produce secondary xylem elements start producing

secondary phloem elements. The cambium cells adjacent to them keep on developing into secondary xylem elements. After some time the cambium cells again start developing into secondary xylem instead of secondary phloem elements. This leads to the formation of islands of secondary phloem [illegible] Such phloem patches are called interx[illegible] The primary xylem is recognisable ne[illegible] secondary xylem ring and consists of distinct metaxylem and protoxylem groups. The included phloem is absent in stems that have not undergone secondary growth.

The cells of the pith next to xylem are small and compactly arranged whereas those towards the centre are large and possess intercellular spaces.

Stem of Calotropis. The stem of *Calotropis procera* (Asclepiadaceae) possesses internal or intraxylary phloem (Fig. 12.22). A cross-section shows the following arrangement of tissues :—

Epidermis. It consists of a single layer of thin-walled cells. The cells are radially elongated A thick cuticle is present. The cuticle is in turn covered with a layer of wax grains.

Cortex. It is composed of several layers of thin-walled cells. The cells are loosely arranged and possess intercellular spaces. The cortical cells contain chloroplasts.

Endodermis. It is the last layer of the cortex. The cells are barrel shaped and possess starch grains. It is also known as starch-sheath.

Pericycle. It is composed of a wide zone of parenchyma with distinct patches or strands of sclerenchyma. The parenchyma cells are compactly arranged and are polygonal in shape.

Vascular Region.

Primary structure. In the young stem there are discrete or separate vascular bundles, each having a phloem towards the outside and patches of internal phloem next to the pith (Fig. 12.22). The primary xylem [illegible] xylem and metaxylem vessels. Tracheids [illegible] present. Xylem fibres are few. The [illegible] tubes, companion cells and phloem parenchyma.

Secondary structure. The cambium [illegible] and divides actively to give rise to s[illegible] the outer side and xylem elements [illegible] secondary phloem is present next to the pericycle and forms a continuous cylinder consisting of sieve-tubes, companion cells, and phloem parenchyma. The primary phloem may persist for some time in the form of small patches. Later on, it gets crushed.

The secondary xylem also forms a continuous cylinder with narrow medullary rays. It consists of vessels, tracheids and xylem parenchyma. The primary xylem is visible in the form of patches next to the pith.

The internal phloem patches are also visible as distinct patches next to the primary xylem.

Pith. It is composed of thin-walled polygonal cells. Latex vessels are numerous in the pith region.

. The xerophytic characteristics of the *Calotropis* stem are :—(*i*) thick cuticle with a layer of wax grains ; (*ii*) radially elongated epidermal cells ; (*iii*) thick-walled patches of pericycle ; and (*iv*) presence of latex tubes.

Stem of Capparis aphylla. It is a common xerophyte belonging to family capparidaceae (dicot). A transverse section of the stem (Fig. 12.23) reveals the following structures :—

Epidermis. It is made up of a single layer of compactly arranged cells. The cells are radially elongated and are covered with a thick cuticle. Its continuity is interrupted by sunken stomata.

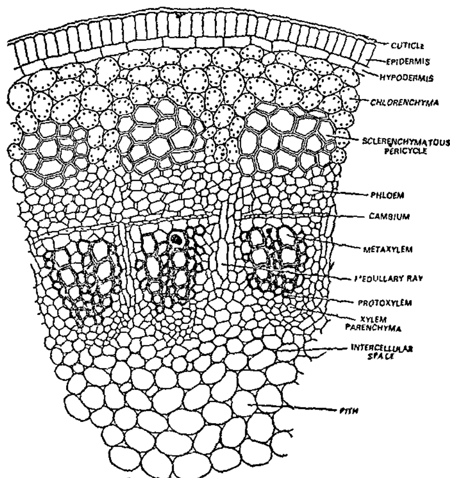


Fig. 12.23. T.S. stem (portion in detail) of *Capparis aphylla* showing primary structure.

Cortex. *It consists of two to three layers of palisade cells.* These cells contain abundant chloroplasts and perform the function of photo-synthesis. The cells are elongated and loosely arranged. They make good the loss of the leaves. The green cells overarch the scleren-chymatous patches of pericycle.

Endodermis. This is not clearly demarcated.

Pericycle. It is both non-fibrous and fibrous. Patches of thick-walled cells alternate with patches of thin-walled cells. The cells are polygonal and compactly arranged.

Vascular System In the primary state, the vascular region consists of a ring of closely arranged discrete vascular bundles. The medullary rays are narrow. The bundles are conjoint, collateral, endarch and open. The phloem has distinct sieve-tubes, companion cells and phloem parenchyma. The cambium is made up of a single layer of rectangular cells. The xylem consists of vessels, tracheids and xylem parenchyma The protoxylem and metaxylem vessels are distinct, the former are smaller in size and towards the pith and the latter are larger in size and towards the phloem.

During secondary growth a complete cylinder of cambium develops. At a later stage a several-layered cambial zone is distinctly recognisable. Actually, the cambium is single-layered but in this case the cells cut off by the cambium develop slowly into secondary vascular elements, thus, making it to appear multi-layered. Distinct stages of

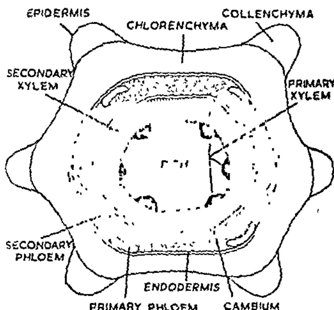


Fig. 12.24. T.S. stem of *Peristrophe bicalyculata* (diagrammatic).

development are recognisable. The cells cut off towards the outer side develop into secondary phloem elements (sieve-tubes, companion cells, parenchyma). The secondary phloem forms a continuous and conspicuous clyinder below the pericycle.

The secondary xylem develops in greater amounts and consists of vessels, tracheids, and thick-walled prosenchymatous cells. Narrow rays aslo develop in the secondary xylem. These appear when the cambial cells give rise to parenchymatous cells instead of secondary xylem elements. The primary xylem is also clearly visible next to the pith. The rays are usually two-or three-layered and consist of radially arranged cells. They connect the pith with the outer tissues.

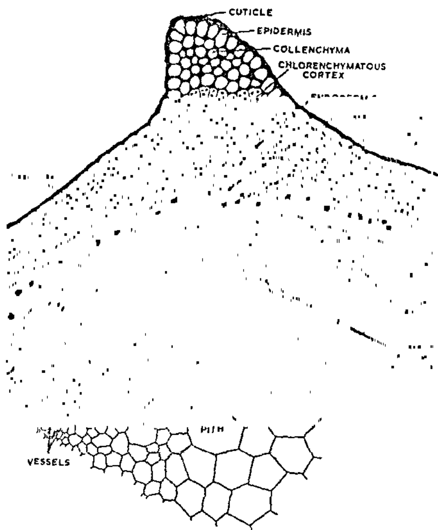


Fig 12 25 T S stem of *Peristrophe bicalyculata* (dicot) showing detailed internal structure.

Pith. It consists of thin-walled cells. The cells are generally polygonal in shape and are compactly arranged. There are small intercellular spaces between them.

The sunken stomata, thick cuticle, radially elongated epidermal

cells, palisade cells, and thick-walled pericycle are the xerophytic characters of the stem.

Stem of Peristrophe bicalyculata (Acanthaceae). It is a much branched, hairy, rough annual herb. The stem is angular and a transverse section usually (Figs. 12.24, and 12.25) reveals six distinct ridges and furrows.

Epidermis. It is composed of a single layer of thin-walled cells. The cells are compactly arranged and covered by a thin cuticle.

Cortex It consists of collenchymatous cells below the six ridges. Next to this are a few layers of oval cells which contain chloroplasts. The cells are loosely arranged and enclose small intercellular spaces. Chloroplasts are absent in the collenchyma.

Endodermis It forms a distinct layer of barrel-shaped cells. Casparian strips are present on the radial walls.

Pericycle. It consists of a few layers of parenchymatous cells. Sclerenchyma is absent.

Vascular System. In the primary state the stem consists of six vascular bundles that are present below the ridges. The bundles are conjoint, collateral, open, and endarch. The phloem, which is present on the outer side only, consists of sieve tubes, companion cells, and phloem parenchyma. Phloem fibres are absent. The cambium consists of a single layer of brick-shaped cells. The xylem shows distinct metaxylem and protoxylem vessels. Tracheids and xylem parenchyma are also present. The vessels are annular and spiral. Reticulate thickenings are present.

During secondary growth a complete ring of cambium is formed. A distinct secondary phloem is visible on the outer side (Fig. 12.25). The secondary xylem shows distinct vessels and forms a continuous band interrupted here and there by narrow rays. These may be uniseriate or biseriate.

Pith. It occupies the centre of the stem and consists of the thin-walled oval or rounded cells. The cells enclose small intercellular spaces.

Stem of Casuarina equisetifolia. The stem of *Casuarina* (Dicot) is thrown into distinct ridges and furrows. A transverse section (Fig. 12.26) shows the following structures :—

Epidermis. It extends over the ridges and furrows and consists of a single layer of compactly arranged cells. Stomata are present in the furrows. A thick cuticle covers the epidermal cells.

Sclerenchyma. It is sub-epidermal and occurs in the form of small patches of thick-walled cells. It is confined only to the ridges.

Cortex. It consists of elongated palisade-like cells in the ridges.

(leaf trace bundles) in the cortex. These bundles are found below the ridges.



Fig. 12.28. T.S. stem of *Casuarina equisetifolia*

Endodermis It is not clearly defined.

Vascular System. It consists of a ring of conjoint, collateral, open, and endarch bundles. The phloem is towards the cortex and consists of sieve-tubes, companion cells, phloem parenchyma, and phloem fibres. The phloem fibres form thick-walled patches at the upper ends of the vascular bundles. A strip of fascicular cambium is present next to phloem.

Xylem consists of vessels, tracheids and xylem parenchyma. Protoxylem is found towards the pith and metaxylem towards the phloem.

The cortical bundles (leaf trace bundles) are conjoint, collateral, and endarch. The phloem fibres occur in the form of patches at the upper ends of the bundles.

Pith. A distinct pith occurs in the centre. It is parenchymatous. The cells enclose intercellular spaces.

The sclerenchyma, thick cuticle and palisade tissue are xerophytic characters of the stem.

Stem of Aristolochia

Primary Structure. A transverse section through the young stem (Figs 12.27 and 12.28) shows the following structures :—

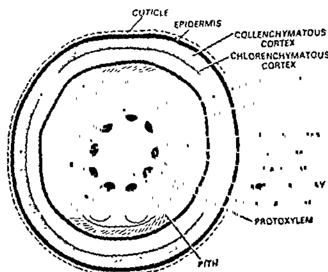


Fig. 12.27. T.S. stem of *Aristolochia* (diagrammatic).

Epidermis. It consists of a single layer of cells and is covered with a thick cuticle. Multicellular epidermal hair are also present.

Cortex. It consists of collenchyma and chlorenchyma. There are two or three layers of subepidermal collenchymatous cells. The walls of the collenchymatous cells possess cellulose thickenings at the angles only. They form one or more uninterrupted layers of living cells

which are devoid of chloroplasts. They are followed by a few layers of thin-walled cells. These contain chloroplasts and enclose small intercellular spaces.

Endodermis. This is the innermost layer of cortex and consists of thin-walled barrel-shaped cells which contain starch grains. They lack chloroplasts and can be easily made out from the chlorenchymatous layers of cortex.

Pericycle. It is distinct as a continuous cylinder of perivascular

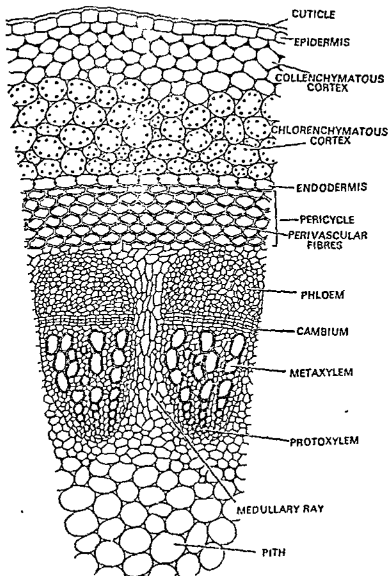


Fig. 12.28. T.S. young stem of *Aristolochia, showing primary structure.* Note the pericycle which is continuous and many-layered and sclerenchymatous.

fibres (Fig. 12.28). The cells have lost their protoplasmic contents and develop thick walls. It forms several layers of cells. In old stems pericycle splits up into separate patches due to the increase in circumference

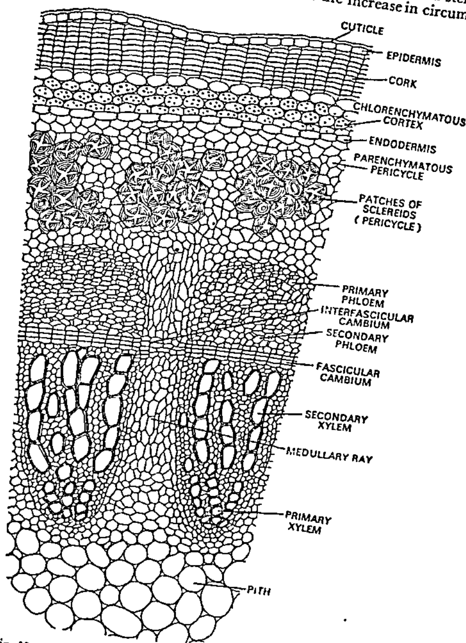


Fig. 12.29. T.S. (portion in detail) of stem of *Aristolochia* showing secondary growth. Note the cork layers, the pericycle splits into groups of sclereids, and the inter fascicular cambium does not produce secondary vascular tissue.

f the axis. It generally ruptures opposite to the rays and the adjacent parenchyma invades these breaks and its cells change into sclereids. Next to the sclerenchymatous ring of pericycle there are a few layers of parenchymatous cells.

Vascular System. It consists of a ring of widely-spaced, conjoint, collateral endarch, and open vascular bundles that surround a parenchymatous pith. The individual vascular bundles are wedge-shaped. The phloem consists of sieve-tubes, companion cells, and phloem parenchyma. Phloem fibres are absent. The sieve-tubes are long and tubular cells with sieve plates on transverse walls. They are accompanied by companion cells. Both the sieve-tubes and companion cells originate from a common mother cell. The phloem parenchyma is abundant. A strip of fascicular cambium, with rectangular cells,

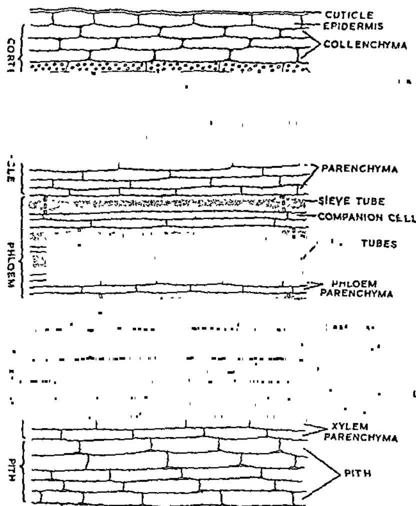


Fig. 12.30. L.S. stem of *Aristolochia.*

arranged in radial rows, is present next to the phloem. It is meristematic.

The xylem is represented by all the 4 elements: (i) vessels, (ii) tracheids, (iii) xylem fibres, and (iv) xylem parenchyma. The vessels can be distinguished into larger metaxylem vessels and smaller protoxylem vessels. Tracheids are also present arround the metaxylem. Xylem parenchyma is abundant and consists of thin-walled living cells.

Medullary Rays. Due to widely spaced vascular bundles the medullary rays are wide and distinct. They consist of thin-walled cells.

Pith. It occupies the centre of the stem and is wide and composed of thin-walled polygonal cells at its periphery and large, rounded cells in the centre. The cells in the centre enclose small intercellular spaces.

Secondary Growth (Fig. 12.29). During secondary growth, the cells of the medullary rays in line with the fascicular cambium become active and start dividing This strip of meristematic cells may be called inter-fascicular cambium. It is not very distinct. The inter-fascicular cambium produces rays which are made up of parenchyma cells only. The secondary vascular elements are produced only by the fascicular cambium (strip of cambium between primary xylem and phloem). This results in the formation of discrete secondary vascular bundles. The cork cambium in this case develops in the collenchyma in the form of isolated vertical strips of meristematic cells that extend from node to node. The cork cambium cuts off cork externally. The

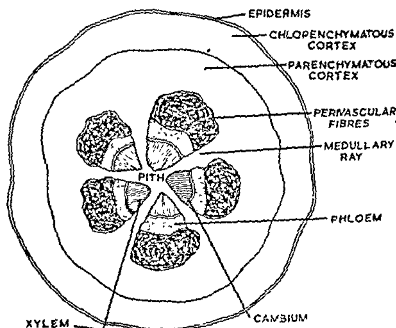


Fig. 12.31. T.S. stem of *Tamarix dioica* (diagrammatic).

continuous layer of sclerenchymatous pericycle splits into groups of sclereids or stone cells. The chlorenchymatous cortex is replaced by ordinary secondary parenchymatous cells derived from phellogen (cork cambium).

Primary structure of stem of Tamarix dioica (Tamaricaceae; Figs. 12.31 and 12.32). A transverse section through the young stem (Fig. 12.31) reveals it to be almost circular in outline. It reveals the following structures :—

Epidermis. It is the outermost layer of thick-walled, rectangular

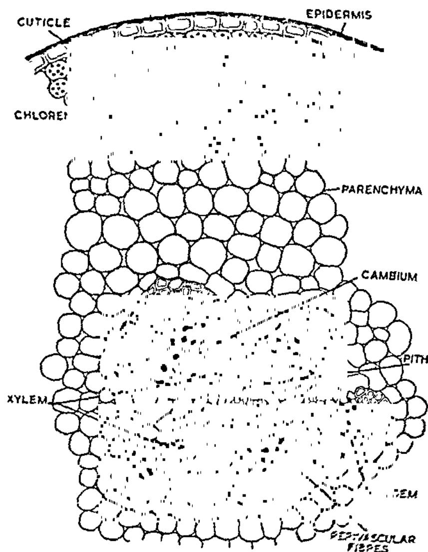


Fig. 12.32. T.S. ... structure. T... and extensive

(in T.S.) cells covered with a thick cuticle. Presence of external glands has been recorded in some species (Sabins).

Cortex. It is distinguished into an outer chlorenchymatous cortex and an inner parenchymatous cortex.

The chlorenchymatous cortex is composed of several layers of thin-walled cells that are packed with chloroplasts. This zone helps in photosynthesis The cells enclose small intercellular spaces.

The parenchymatous cortex is also composed of several-cell layers. The cells are filled with abundant tannin. They are almost circular (in T.S) in outline and enclose small, intercellular spaces. In some species, groups of sclereids also occur in the cortex. The endodermis is not recognisable.

Pericycle. It occurs in the form of patches of thick-walled cells lying external to the phloem In *T. gallica* and some other species, the sclerenchymatous pericycle forms a continuous ring in young stems.

Vascular Region. It consists of a ring of 5 or more vascular bundles separated by broad medullary rays. The bundles are conjoint, collateral, open and endarch. The phloem consists of **phloem fibres, sieve-tubes, companion cells** and **phloem parenchyma.** It is followed by a single layer of cambial cells. The xylem constitutes a large portion of the bundle and consits of vessels with simple perforations, tracheids with a few simple pits on radial walls and some xylem parenchyma.

Pith. It is small and consists of thin-walled or thick-walled cells filled with tannin and crystals of gypsum.

PRIMARY STRUCTURE OF MONOCOTYLEDONOUS STEMS

The monocotyledonous stems differ in certain respects from the dicotyledonous stems. These differences will become evident after studying the anatomy of a few examples of monocot stems.

Maize Stem (Indian corn)

A transverse section of the maize stem (*Fig. 12.33*) reveals the following tissues from outside within :—

Epidermis. It forms the outermost boundary of the stem and is made up of a single layer of cells with their outer walls covered with a thick cuticle. The continuity of this layer may be broken here and there by presence of a few stomata.

Hypodermis. A few layers of sclerenchymatous cells lying below the epidermis constitute the hypodermis. There are usually two or three layers of hypodermis cells whose walls are lignified. In a cross-section, the cells appear to be polygonal in shape. This layer gives mechanical strength to the stem.

Ground Tissue. There is no distinction into cortex, endodermis pericycle and pith. The entire mass of parenchymatous cells lying next

to the hypodermis forms a ground tissue. The cells have cellulose walls and contain reserve food-materials like starch. The cells of the

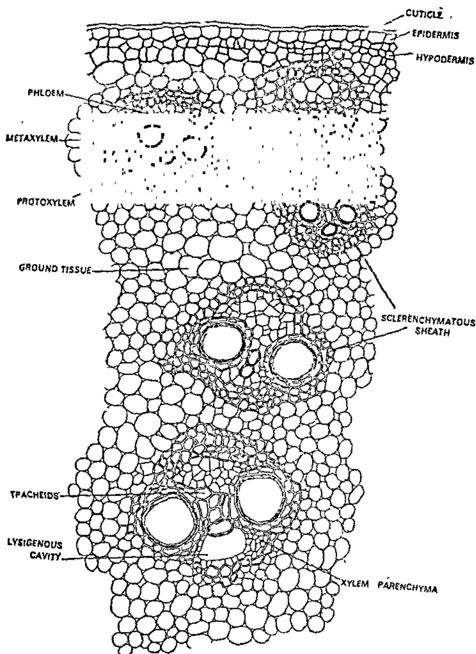


Fig. 12.33. T.S. portion in detail of stem of *Zea mays* (Monocot) showing internal structure. Note the incomplete peripheral vascular bundle below the hypodermis. The lysigenous or water cavity is also absent in the outer bundles. It is found only in the central vascular bundles (A Camera lucida drawing).

ground tissue next to the hypodermis are small in size, polygonal in shape (in a cross-section) and are compactly arranged. Towards the centre, the cells become loosely arranged, rounded in shape and have bigger size The vascular bundles lie embedded in this tissue.

Vascular system. The vascular region consists of numerous vascular bundles that are scattered (Fig. 12.33) in the parenchymatous ground tissue. The monocotyledonous stems are characterised by this scattered arrangement of the vascular bundles. This arrangement is, however, lacking in the runners and erect stems of grasses. Such a scattered distribution of vascular bundles in the monocot stems is on account of the leaf trace bundle entering the stem at various levels towards the centre. These leaf trace bundles then curve outwards and meet near the periphery. Before coalescing, the leaf trace bundles are recognisable as independent units through the internodes and this results in the charactistic scattered arrangement.

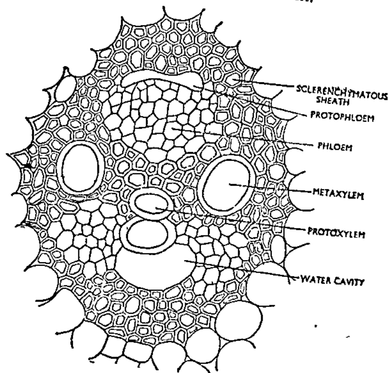


Fig. 12.34. A vascular bundle of maize stem (Monocot) as seen in a cross-section.

Each vascular bundle is surrounded by a sheath of sclerenchymatous fibres (Figs. 12.33 and 12.34). The sheath is extensively developed at the upper and lower faces of the bundles. The vascular bundles are **conjoint, collateral, endarch**, and **closed** (because there is no cambium).

They are numerous and closely arranged in the peripheral portion. Towards the centre, the bundles are comparatively large in size and loosely arranged. The vascular bundles are almost oval in outline (Fig. 12.33) and consist of phloem and xylem.

Pholem. The phloem in the monocot stems is [illegible] of sieve-tubes and [illegible] fibres are abser[illegible] **proto-phloem** and a [illegible] metaphloem [illegible] latter is the functional part of the phloem in mature vascular bundles and shows distinct sieve-tubes and companion cells.

Xylem. The xylem consists of both protoxylem and metaxylem vessels, tracheids and xylem parenchyma. The metaxylem and protoxylem elements present the shape of an English letter, 'Y'. The divergent ends of the 'Y' are occupied by two big, oval metaxylem vessels (*Fig. 12.34*) *constituting the metaxylem. Their walls have pitted* thickenings. In-between them are present smaller, polygonal, metaxylem tracheids that also have pitted thickenings. The protoxylem which is positioned radially towards the centre (occupying the lower arm of the 'Y') consists of two smaller vessels with annular and spiral thickenings. The protoxylem elements are partially surrounded by metaxylem tracheids and partially by xylem parenchyma. The latter almost surround a conspicuous water-containing cavity (Fig. 12.34) also known as lysigenous cavity (because it is formed lysigenously by the breaking down of inner protoxylem vessels and parenchyma). Xylem fibres are present in smaller numbers along with the metaxylem tracheids.

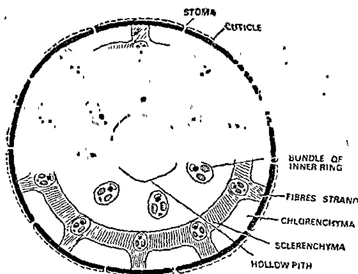


Fig. 12.35. T.S. of stem of *Hordeum vulgare* (Barley) (diagrammatic).

Stem of Grasses (Monocot). The grasses present a distinct pattern of the mechanical tissue in the stems. Sabins (1921) described the

various grasses on the basis of distribution of mechanical tissue in the leaf and stem. Banerji and Swamminathan (1964) were able to utilise anatomical features in wheat stem and coleoptiles to distinguish between the various sub-species of *Triticum aestivum*.

Hordeum (Barley). In transection (Figs. 12.35 and 12.36) the stem of *Hordeum* presents a circular outline. The stem is hollow.

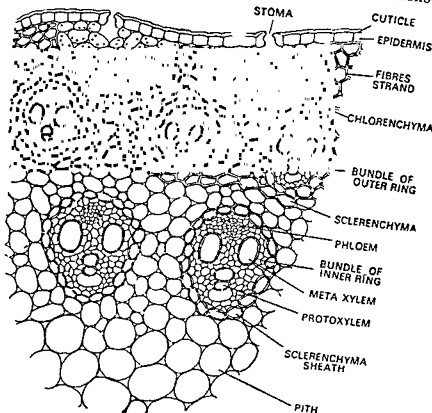


Fig. 12 36 T.S. of a portion of stem of *Hordeum vulgare*, showing detailed internal structure.

Epidermis It is made up of a single layer of cells and is interrupted by stoma. A distinct cuticle is present.

Sclerenchyma. In *Hordeum* the sclerenchyma or the ring of mechanical tissue is free from epidermis. It is a continuous ring of thick-walled cells. A number of vascular bundles lie embedded in it. These bundles form the outer ring. Each embedded vascular bundle is connected with epidermis by means of a group of fibre strands. These fibre strands alternate with chlorenchymatous groups of cells. These cells contain chloroplasts andthe stomata usually lie in the portion of the epidermis adjoining chlorenchyma (Fig. 12.36).

Ground Tissue. Next to the sclerenchymatous ring the stem contains the ground tissue, which is composed of thin-walled cells. In this tissue lies embedded the second ring of vascular bundles.

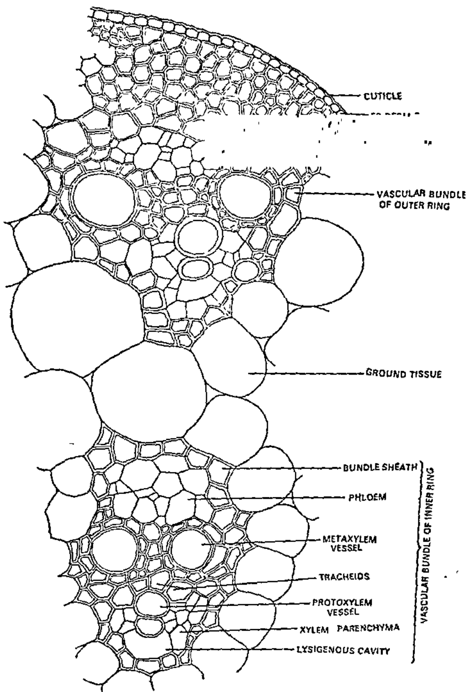


Fig. 12 37. T.S. portion of stem of grass (Cynodon dactylon), showing detailed internal structure.

Vascular System. There are two rings of vascular bundles. The outer ring is embedded in the sclerenchyma and the inner ring is embedded in the parenchymatous ground tissue. Bundles in both the rings are conjoint, collateral, endarch, and closed. The vascular bundles are surrounded by a sclerenchymatous sheath. The vascular bundles are oval in shape and those of the inner ring are larger in size. The phloems consists of sieve tubes and companion cells. Phloem parenchyma is absent. The xylem has two conspicuous, larger, and oval vessels of metaxylem and a smaller vessel of protoxylem. They are arranged in the form of a 'V'. The metaxylem vessels show pitted thickenings whereas the protoxylem vessels have spiral and annular thickenings. Between the two metaxylem vessels pitted trachleids also occur. Xylem parenchyma is also present. Some of the protoxylem vessels break down to form the lysigenous cavity.

The stem is hollow.

Similar strurcture is shown by the stems of *Triticum* (wheat), *Avena* (Oat), *Oryza* (Rice Fig. 12.38), *Secale* (Rye), and many other grasses.

Stem of Asparagus. A transverse section (Fig. 12.39) through the stem of *Asparagus* (Liliaceae, Monocot) displays distinct ridges and shows the following tissues :—

Epidermis. It is covered with a cuticle and consists of compactly arranged thin-walled cells. The cells of the epidermis in the ridges are exceptionally large in size and quite distinct from the neighbouring epidermal cells. These cells look like motor cells or buliform cells in shape, but do not have the same function. Stomata are present in the epidermis.

Cortex. It forms a few layers of thin-walled cells below the epidermis. The cells are polygonal or rectangular in shape and contain chloroplasts. The cells enclose intercellular spaces. It is composed of two to three layers below the grooves but it is many-layered below the ridges. It performs photosynthetic functions.

Endodermis. It is the innermost layer of cortex and consists of closely arranged thin-walled cells. The cells contain starch and lack chloroplasts. Casparian strips are not distinct.

Pericycle. It forms several layers of sclerenchyma cells forming a continuous cylinder below the endodermis. It gives mechanical strength to the stem and is well-developed.

Ground tissue or pith. Next to the pericycle is the ground tissue, which can be designated as pith since there is a clear demarcation between it and cortex. This is due to the presence of endodermis and pericycle. In it lie embedded numerous scattered vascular bundles. The cells are thin-walled.

Vascular System. Like all other monocots it is composed of discrete vascular bundles that are scattered in the central ground tissue. The bundles near the periphery are smaller in size and those in the

centre are larger. The bundles lack a sclerenchymatous sheath and are conjoint, collateral, endarch and closed. The xylem forms a 'V'. The metaxylem vessels occupy the arms of 'V' and the protoxylem

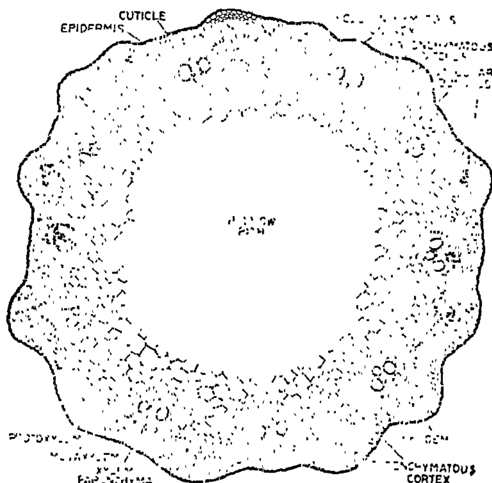


Fig. 12.38 T.S. stem of *Oryza sativa*
Note the hollow pith.

occupies the angle. There is no lysigenous cavity and *protoxylem* is well-developed. The xylem consists of vessels. tracheids and parenchyma. The metaxylem ... vessels. The vessels in ... The phloem is enclosed ... and consists of *sieve* tubes, companion cells and a little parenchyma.

The thick pericycle and chlorophyllous *cortex are the* xerophytic characters.

Stem of Tamus communis. It is *monocot* stem that exhibits regular arrangement of the vascular bundles that are found in rings (Fig. 14.20). A transverse section of the stem reveals the following structures :—

Epidermis. It consists of a single row of small cells, that are compactly arranged and are covered by a thin layer of cuticle.

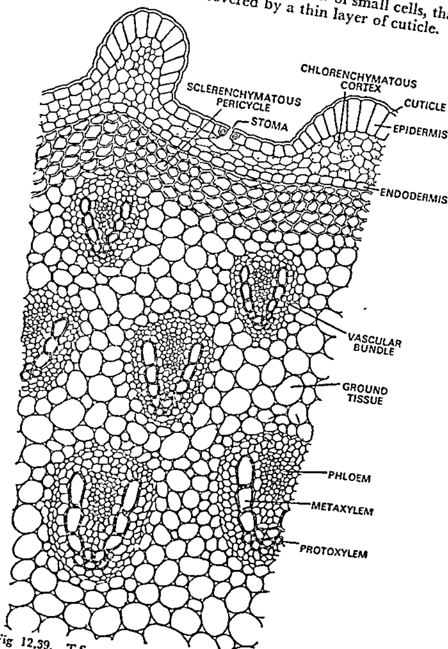


Fig 12.39. T.S. portion of stem of *Asparagus*. Note the ridges.

Cortex. There is a well-defined cortex in *Tamus*. It consists of a few layers of oval or elliptical cells that are loosely arranged and enclose numerous intercellular spaces. Presence of a definite cortex in a monocotyledonous stem is also an anomaly in itself especially when there is a well-defined endodermis and a pericycle.

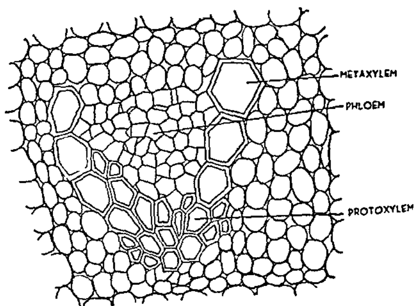


Fig. 12.40. Vascular bundle of *Asparagus*.

Enodermis. It consists of a single layer of barrel-shaped cells.

Pericycle. It is composed of two or more layers of sclerenchymatous cells, that are uninterrupted and form a continuous cylinder around the central pith or ground tissue.

Vascular system. It consists of two rings of vascular bundles. They are not scattered and are arranged regularly in two rings, an anomalous feature for the monocots. The outer ring consists of smaller vascular bundles originating in the pericycle. The inner ring consists of larger bundles that are not surrounded by any sclerenchyma sheath. The bundles are collateral, endarch, and closed. The xylem is in the form of 'V'. The metaxylem vessels occupy the arms of 'V' and are larger in size. Their walls have simple pits. The protoxylem occupies the vertex of the 'V' and has spiral and annular thickenings. Phloem lacks phloem parenchyma and phloem fibres. It consists only of sieve-tubes and companion cells.

Pith. There is a distinct pith in the centre. It consists of rounded and thin-walled cells which enclose distinct intercellular spaces.

This stem resembles the monocots in possessing closed vascular bundles. It resembles dicots in possessing regular arrangement of vascular bundles, distinct cortex, endodermis and pericycle.

The stem of *Asparagus* reveales a few differences from that of maize stem. These can be listed as :—

(1) After the epidermis the ground tissue is distinguished into cortex and a several-layered band of sclerenchymatous pericycle ; (2) the hypodermis is absent ; (3) the vascular bundles lack a sclerenchymatous sheath ; and (4) there is no water-containing cavity.

Peduncle of Canna.

A slightly different pattern is presented if we examine transverse section through the flowering stem of *Canna* (Fig. 12.41). In this case, epidermis is followed by two to four layers of cortical parenchyma,

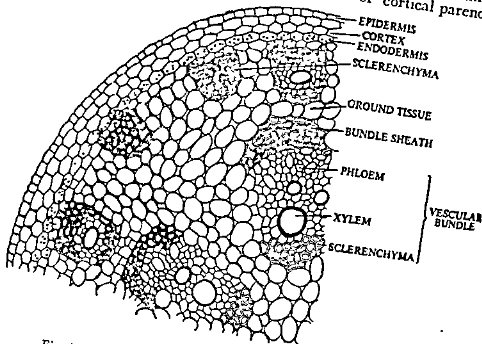


Fig. 12.41. T.S. through a flowering stem of Canna (Monocot), showing details of structure. Note the sclerenchyma sheath restricted only to the two ends of the vascular bundles. The water cavity is absent.

whose last layer may be regarded as an endodermoid layer. After this layer are alternating patches of sclerenchyma and parenchyma which constitute the pericycle. Next to the pericycle is a continuous mass of parenchyma which makes up the ground tissue in which lie embedded various vascular bundles in an irregular manner. The vascular bundles are conjoint, collateral, closed and endarch and are of varying sizes. The sclerenchymatous sheath, caps the vascular bundles at their outer and inner sides. The arrangement of the xylem vessels is different. There is a single, large and prominent vessel lying towards the inner side. Its walls have spiral thickenings. One or two smaller vessels are present towards the outer side (towards phloem). Their walls also possess spiral thickenings. Xylem parenchyma is also present. Tracheids and wood fibres are indistinguishable. Water cavity is absent. Phloem is on the outer sides of the xylem and consists of only sieve tubes and companion cells. Protophloem is absent, perhaps its cells become lignified and add to the sclerenchymatous cap.

In *Commelina*, the epidermis is interrupted by stomata and is followed by a few layers of thick-walled hypodermis, next to which are

2—5 layers of chlorenchymatous cortex. Endodermis is distinct and is composed of a single layer of barrel-shaped cells. The *pericycle* is made up of several layers of sclerenchymatous cells. There is a distinct *pith* or ground tissue in the centre. *It is made up of parenchymatous* cells.

There are two types of vascular bundles :—

(*i*) **Peripheral bundles.** They are present in the *pericycle region* and are surrounded by a distinct sclerenchymatous sheath. The xylem is 'V'-shaped. There is no lysigenous cavity.

(*ii*) **Medullary bundles.** There are numerous bundles *scattered in the* ground tissues. These are comparatively small and less *developed. They* are not surrounded by a sclerenchymatous sheath and the xylem is reduced to a single vessel with xylem parenchyma all *around it.*

13

THE STEM—SECONDARY GROWTH

The growth in length of the axis is called the primary growth and produces primary tissues. It is effected by the activity of the apical meristems. [illegible] ss only primary growth. Ir [illegible] shrubs) dicots, and in ma [illegible] and stem axes continue to grow not only in length but in diameter also. The increase in girth or thickness of the axis is called the secondary growth and is accomplished chiefly by the activity of another meristem quite different in character, the *vascular cambium.* The vascular cambium, which arises between the xylem and the phloem, contributes not only to the thickness of the axis but may, to some extent, be observed in the petioles [illegible] *Aloe, Cordyline,* [illegible] also exhibit [illegible] dary growth of the axis includes within its activities the formation of additional vascular tissue (seconoary xylem and phloem) and the *periderm.* The detailed accounts of the structure and development of vascular cambium and periderm have been given in chapters 8 and 9. *Secondary growth can be defined as an increase in the diameter of the axis, as a result of the activities of the lateral meristems (vascular cambium and cork cambium), which cut off secondary tissues in the stelar and the extra-stelar regions.*

The process of secondary growth in a dicot stem can be studied under the following headings :—

Activity of the cambium. The cambium is made up of two dissimilar types of cells corresponding to the longitudinal and transverse cellular systems in vascular tissue. Those cambium cells that produce tracheids, fibres, sieve-cells, and other elements of the [illegible] usually much

[illegible] ambium develops into a [illegible] between the

[illegible]

become [illegible]

strips join with the strips of fascicular cambium and thus form a complete ring of cambium (Fig. 13.1. A, B).

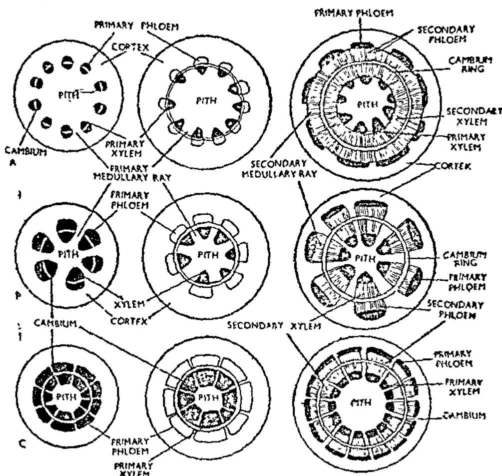


Fig. 13 1. Secondary growth (A—C), Three types of secondary growth in dicotyledons; A, Sunflower type. B, *Aristolochia* type. C, *Linum* type (Diagrammatic).

In some dicots e.g., *Linum* and *Tilia*, the primary xylem and phloem are not visible in the form of discrete or separate vascular bundles and appear in the form of a closed cylinder [illegible] ses, the **fascicular** cambi[illegible] and no new [illegible] interfascicular cambium [illegible] 3.1 C). Its a [illegible] whole circ[illegible]

In *Aristolochia*, the primary vascular bundles are quite separate (Fig. 13.1. B) and new strips of interfascicular cambium are formed to form a complete ring of cambium. In this case, the interfascicular cambial strips do not produce secondary vascular tissues with the result that vascular bundles maintain their discreteness throughout the secondary growth. Secondary vascular tissues are produced only

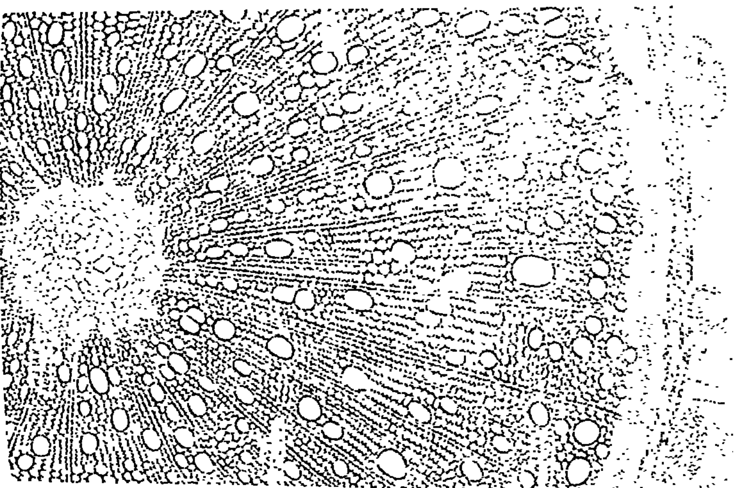


Fig 13 2. T.S. Stem of *Dalbergia sissoo*, showing secondary growth. The wood is ring porous.

by the **fascicular cambium**, which is present between the primary phloem and xylem.

After the maturation of primary xylem and primary phloem in the vascular bundles of dico the cambial cells begin to divide valls appear in such a way as to cut ( ) the outside of the cambium. The new cells formed on the side of the cambium facing the primary xylem mature into the elements of **secondary xylem** (Fig. 9.4). The new cells formed on the side of cambium facing the primary phloem mature into the elements of **secondary phloem.** When the cambium cell divides by a tangential wall into two cells, one of them functions as cambium and the other either changes into xylem or phloem elements. If the new cell produced by such a division on the outside becomes cambial, the one towards inner side functions as cambial cell, the outer daughter cell functions as phloem mother cell (Fig 9.4). Cambium is generally a single layer of cells, but it appears many-layered if the mother cells of xylem and phloem are formed rapidly and do not immediately change into the respective elements *e.g.*, *Tilia*, *Vitis* etc. Since cambium forms a continuous ring, the secondary phloem and the secondary xylem assume the form of concentric cylinders continuous except where they are penetrated by rays.

Cambial cells adjacent to the rays (ray-initials) produce additional parenchymatous cells to the inside and to the outside, thus, extending rays through new secondary xylem and phloem and maintaining, at least for a time, vertical plate-like connections between the pith and the cortex. These parenchymatous plate-like extensions are called **secondary medullary rays**, which are one to a few layers in thickness and from one to several layers in height. As the secondary xylem cylinder expands, there must be a compensating expansion of the cambium in order that this meristematic layer be maintained as an unbroken cylinder. Such an increase in the circumference of the cambial ring is accomplished by an increase in total number of cambial cells due to occasional radial divisions in addition to the usual tangential divisions. More commonly, however, the cambial cells divide by an obliquely radial (pseudotransverse) wall, and the daughter cells move past one another until the two initials reach normal length and lie side by side tangentially. The number of such divisions is usually more than enough to make the number of cambial cells conform to the enlarging circumference of the cambium (Bannan, 1953), process known as **dilation.**

In most of the herbaceous dicots such as alfalfa (*Medicago sativa*) the cambium ordinarily produces secondary xylem and secondary phloem only for one season after which aerial stem dies. In the woody dicots (trees, shrubs) the cambium remains active for years together and secondary xylem and secondary phloem are formed every year. It has been observed that the amount of secondary xylem produced is much more than that of secondary phloem.

The formation of secondary vascular tissue in-between the

primary phloem and the primary xylem isolates the latter from the former and produces considerable stress on the interior of the stem. Due to the excessive production of secondary xylem or secondary wood, the primary xylem and the pith are covered by the secondary xylem. For some time, the primary xylem remains unchanged in position and form and the primary xylem parenchyma cells may remain alive for many years. The primary xylem is generally recognisable in the form of conical protuberances in the pith. As the amount of secondary xylem produced increases, the primary xylem and pith are deformed. The primary xylem elements become non-functional. Ultimately, the whole of the central cylinder consists only of secondary xylem.

The formation of secondary phloem causes displacement of the primary phloem towards the outside. Ultimately, the primary phloem elements become non-functional and in most of the dicots change into fibres. Phloem parenchyma and sieve-elements get crushed. The cells in the cortex divide anticlinally and increase in circumference thus keeping pace with the increasing width of the secondary tissue. It may, in this way, keep on increasing its circumference and persist for years. Ultimately, it also fails to conform with the growing circumference of the secondary wood and gets crushed or broken here and there. The same is the case with the epidermis. It also increases in circumference by the anticlinal divisions of its cells but may ultimately rupture

The secondary phloem is also subjected to considerable pressure as a result of the formation of large amounts of secondary wood. In *Tilia* and other dicots (Fig. 13.4), the old non-conducting phloem is not crushed because the phloem parenchyma cells and cells in the rays can accommodate the increasing circumference of the secondary wood by the division of their cells. In *Tilia*, specially, the cells in the secondary medullary rays undergo growth and division and as a result the rays in the phloem region increase in width and become dilated (Fig. 13.4). The major portion of the secondary vascular cylinder is made up of secondary xylem or wood. Secondary phloem is not so well-developed and is generally termed as bast.

SECONDARY XYLEM

The main difference between the primary and the secondary xylem is that the former is derived from the procambium and the latter develops from the vascular cambium. So far as the cell types are concerned, they are similar in both the primary and secondary xylem. There is no distinction into proto-and meta-xylems in the secondary xylem. The primary xylem elements are generally longer than the secondary xylem elements. The secondary xylem shows a clear distinction into **axial** and **radial systems**. This type of distinction is absent in the primary xylem. The **axial system** is made up of vertical rows of cells with their long axes parallel to the long axis of the organ, in which they are present. It consists of vertical files of **tracheids**, **vessels, xylem fibres** and longitudinal rows of **xylem parenchyma cells**. The **radial system** is made up of rows of chiefly parenchymatous

cells that are oriented horizontally with regard to the axis of the root or the stem. It is chiefly made up of **xylem rays** or **wood rays.** In a transverse section of the stem, the cells of the axial xylem are cut transversely, whereas those of **radial system** are cut length-wise. In a radial section (L.S. cut parallel to the radius of the organ), the cells of the axial system reveal their longitudinal extent whereas the cells of the radial system appear as horizontal bands lying across the axial system. In a tangential section (cut perpendicular to the radius), all the axial cells are cut length-wise and the cells of radial system are cut perpendicular and reveal their height and breadth.

The xylem vessels may occur singly in *Rosa* (Fig. 13.7) and *Dalbergia* (Fig. 13.2) or in linear rows as in *Eugenia* and *Cassia* (Fig. 13.5 and 13.9) or in irregulur groups.

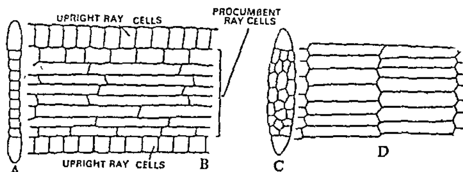


Fig. 13.3.

Exclusive of vessels and tracheids the remaining of the secondary xylem in dicot stems is made up chiefly of elongated empty cells with pointed ends and thick walls. These cells which give mechanical strength to stem are called the **xylem fibres** or **wood fibres** ; **xylem parenchyma** or **wood parenchyma** is also present*e. g.*, in walnut, parenchymatous cells are numerous. In the secondary wood of willows and cotton the parenchymatous cells are a few in number. In *Eugenia jambolana* and *Poinciana regia*, the xylem parenchyma is associated only with the vessels. In the stem of *Azadirachta indica*, the xylem parenchyma is distributed among xylem fibres. These cells store reserve food materials like starch. The distribution of xylem parenchyma with respect to the vessels has been discussed in chapter 5 (Fig. 5.10).

Xylem Rays. The xylem rays ar
These may be from few to many layei
radial conduction of water and diss
outer tissue. The xylem rays are
traverse radially the secondary xylem and are continuous throughout the cambium into the secondary phloem. They are also known as vascular rays. The portion of these rays confined to the secondary

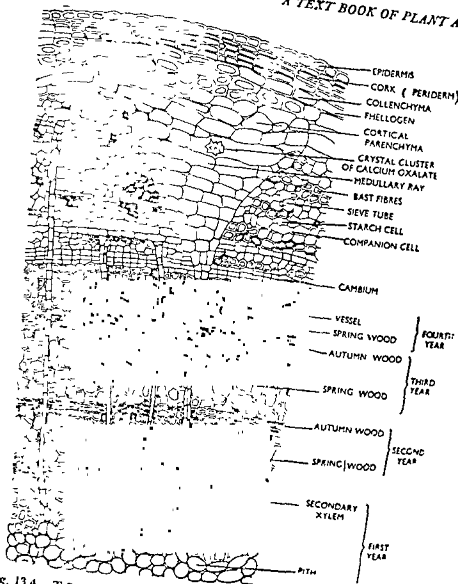


Fig. 13.4 T.S 4-year old stem of *Tilia* showing distinct annual rings. Also note the dilated secondary medullary rays near the phloem. The oldest phloem in this case remains uncrushed and changes into bast fibres The secondary xylem portion shows ring porous wood.

xylem is called the **wood ray** or **the xylem ray**. The portion confined to the phloem is called **phloem ray**. The cells comprising these rays maybe thin-walled or may be lignified. The former store starch, oils and variety of ergastic substances. The lignified cells have bordered or simple pits The rays are of two types :—

1. **Homocellular rays.** These are made up of one type of cells (Fig. 13.3).

2. **Heterocellular rays.** These are made up of two types of cells (Fig. 13.3) :—

Fig. 13 5. T.S. stem of *Eugenia jambolana* showing secondary growth Note the inner phloem and the sclerenchymatous patches internal to this. The pith cells also possess sphaeraphides. The secondary vessels occur in groups and form oblique lines. The wood is diffuse porous. Note the secretory canals in the cortex. Sphaeraphides are present in the cortical as well as pith cells.

(i) **Procumbent cells** are those whose longest diameter is oriented radially.

(ii) **Upright cells** are vertically elongated.

The vascular rays may be *uniseriate* if they are one cell in width (Fig. 13.3) and *multiseriate* if they are two or more cells in width (Fig. 13.3). They are termed as biseriate if two cells in width. The multiseriate rays appear fusiform in a transverse section. The height of both the types of rays varies greatly. They may be short or long.

The vessels in the secondary wood usually possess pitted thickenings and are comparatively shorter than the primary xylem. Their main function is conduction of water and minerals dissolved in it.

Annual Rings. The activity of vascular cambium is markedly effected by variations in the climate. In those regions of the world e.g., temperate regions, where the changes in the climate in different parts of the year are pronounced, the cambial activity varies. During the winter, the cambium stops dividing. In the spring season, it regains its activity and starts dividing. During this season, vegetative growth of the trees is pronounced, more leaves appear, and there is dire need of efficient transport of water and minerals dissolved in it and of food materials so that the plant can cope with its increasing requirements. The cambium becomes more active because of favourable environments and divides actively producing a large number of vessels that have wider lumens. The secondary xylem formed during this period of pronounced activity is called **spring wood** (Fig. 13.2). During the autumn season the activity of the cambium is lessened and the vessels produced are generally of smaller size and have narrow lumens. Tracheids and wood fibres are produced in large numbers (Fig. 13.2). The secondary wood formed during this season of the year is called **autumn wood or summer wood.** In a transverse section of the stem, these two types of wood appear in the form of distinct concentric circles known as the **annual rings.** Springwood circle and autumn wood circle constitute an annual ring. Like this, year after year, such rings appear and their identity is well-marked. The number of annual rings in the oldest part of the tree corresponds to its age. In some woody trees e.g., *Tilia* (Fig. 13.4), black ash, *Cassia fistula* (Fig. 13.9), *Dalbergia sisoo* (Fig. 13.2), and *Tamarix dioica* (Fig 13.6), the vessels in the spring wood are large and arranged in a ring and narrow vessels of the summer or autumn wood are scattered. Such a wood is said to be **ring porous** (Fig. 13.3). In *Eugenia jambolana*, (Fig 13.5), *Rosa* (Fig. 13.7), *Sambucus* and *Azadirachta indica*, the vessels are more or less uniformly distributed throughout the spring wood and autumn wood. Such a wood is called **diffuse porous wood.** However, in the wood produced towards the end of the growing season, there is a larger proportion of the elements other than vessels. Hence even though the vessels throughout each annual ring are more or less alike and uniformly distributed, a notable difference exists between the late summer wood of one year and the spring wood of the following year to clearly demarcate one ring from another.

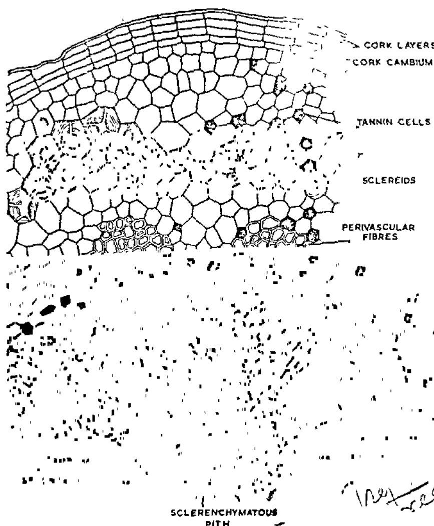


Fig. 13.6. T.S. portion of stem of *Tamarix dioica*, showing secondary growth (one-year old branch). The wood is ring porous.

The annual rings or the growth rings are not well-marked in the trees growing in the tropical regions of the world. Here the number of growth rings does not correspond to the age of the tree. Such growth rings have been given the name of **Growth marks**. In *Garuga pinnata* the shoot, due to uniformity of the season, does not even show the growth marks.

The thickness of the annual rings is greatly influenced by fluctuations in the environmental conditions. Variations in the thickness of the annual rings have been correlated with weather variations as a result of observations made by weather bûreaus in various parts of the world. It has been found out that the annual rings remain thin during low rainfall and become thick if the rainfall is heavy. Sometimes, permanent changes are brought about in the environment by chopping down

the trees or by draining away water. In such cases the thickness of the rings produced before and after the change is remarkable and it has been possible to exactly judge the year when such a change was brought about.

Dendrochronology. Determination of age of a tree by counting the annual rings is termed **dendrochronology**. The number of annual rings enables us to count with considerable accuracy the age of a tree. Sections at the bases of shoots in American Sequoiadendron, with the

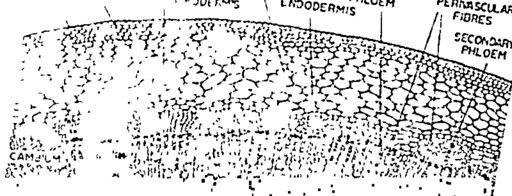


Fig. 13.7. T.S. stem of *Rosa* showing secondary growth. Note the scattered sclerenchymatous elements in the pith. The wood is diffuse porous.

shoot reaching 5—6 metres in diameter, have revealed them to be upto 3,500 years old.

The annual rings do not always give us the exact age of a tree because it is not unusual that sometimes two rings are formed in a single year. It is perhaps due to interpolation of dry period in the middle of a growing season. In this case, dry weather xylem resembles summer wood. At the end of this interpolated dry weather again favourable weather starts and the xylem vessels produced resemble spring wood. Again, at the end of the growing season the vessels produ... ear.

Sa... d secondary growtl... m and its old branches have a part of its secondary xylem rendered non-functional.

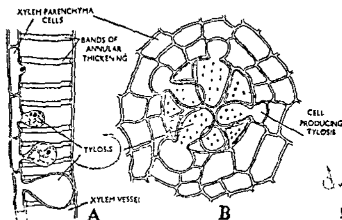
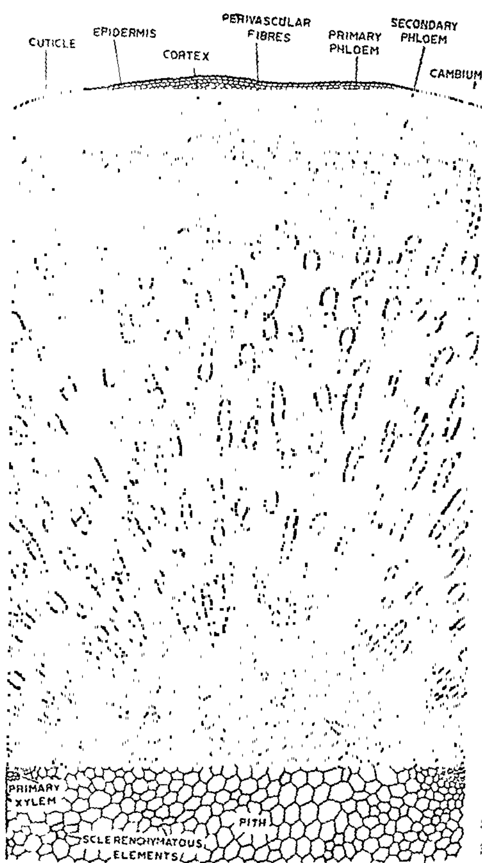


Fig 13 8. (A,B). Tyloses. A, L.S xylem vessel showing development of tylosis, B, same as A in T.S.

... els and tracheids ... produced by adja- ... 's of many woody ... on-functional and surrounding parenchyma cells also die. This usually results in the darkening of the cell walls with the result that the central core of non-...

addition of new outer rings of secondary xylem more rings of the sap wood are changed into heart wood. This leads to the increase in the thickness of heart wood, whereas the sap wood remains of about the


CUTICLE
EPIDERMIS
CORTEX
PERIVASCULAR FIBRES
PRIMARY PHLOEM
SECONDARY PHLOEM
CAMBIUM
PRIMARY XYLEM
PITH
SCLERENCHYMATOUS ELEMENTS

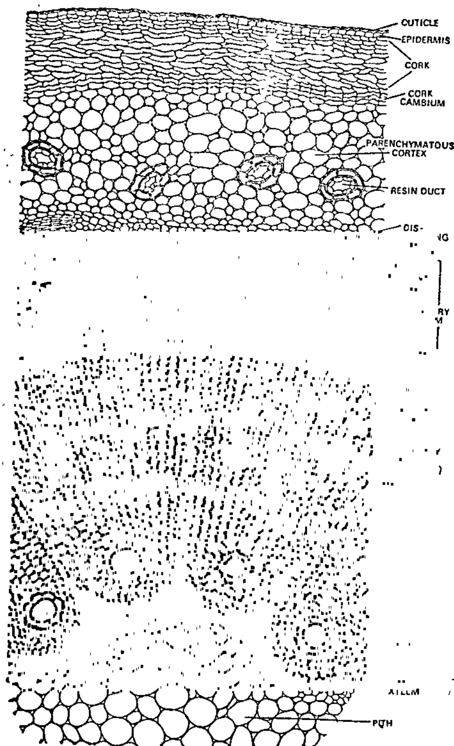


Fig. 13.10. T.S. stem of *Pinus roxburghii* showing secondary growth.

same thickness In some dicots like *Populus* and *Salix*, there is no heart wood. In *Morus alba* the sap wood is less developed, and heart wood is well-developed. In *Tamarix*, *Acer* and *Fraxinus*, the sap wood is well developed and heart wood is narrow.

SECONDARY PHLOEM

In the dicot stems the secondary phloem consists of sieve tubes, companion cells, phloem parenchyma and phloem fibres. In some plants the phloem fibres may be absent. The sieve tubes possess sieve plates which may occur only on the end walls or on both the end walls and the walls of their segments. Companion cells always accompany the sieve-tubes in the dicot stem. Parenchyma cells with reserve food material are also present. Phloem fibres, which are thick-walled, elongated cells with tapering end walls also occur in the secondary phloem of woody dicots and gymnosperms. They constitute the bast fibres.

The sieve plates are of two types. They may be simple as in most woody plants. Compound sieve plates occur in the secondary phloem of *Tilia* and *Vine*. The amount of phloem parenchyma varies with species. In *Zizyphus* (Beri) the parenchyma cells contain crystals and occur in the form of alternating bands of cells on either side of the sieve-tubes. The secondary phloem of *Hevea braziliensis* and *Lactuca scariola* contain laticiferous vessels. Occurrence of sclereids has also been reported in the secondary phloem.

The sieve-tubes become nonfunctional by the development of a pad of wall material over the sieve plates. It generally happens at the end of a growing season. Such a nonfunctional phloem may get crushed during the next growing season due to the expanding cylinder of newly formed secondary xylem and phloem. In *Tilia*, the elements of this nonfunctional phloem change into bast fibres (Fig. 13.4), which resist the crushing effect and remain unchanged for several years.

The function of the secondary phloem is similar to that of the primary phloem and affords conduction of the food materials like proteins and carbohydrates. The secondary medullary rays in the region of the secondary phloem permit radial conduction of water from the xylem. In Eugenia (Fig. 13.5), there is inner phloem also.

Periderm. For a detailed account refer to chapter 10.

SECONDARY PHLOEM AND SECONDARY WOOD OF GYMNOSPERMS

The secondary phloem of gymnosperms consists of sieve-tubes, phloem parenchyma and phloem fibres. Companion cells are absent. The sieve plates are present on the lateral walls. The phloem fibres and phloem parenchyma are present in smaller amounts. The parenchyma cells occur in longitudinal rows and store reserve food material and also contain resins, crystals and tannins. The phloem rays in the gymnosperms are characteristic in that they contain specialised cells called the albuminous cells on the upper and lower margins of the secondary phloem rays. These cells contain dense cytoplasmic contents and

distinct nuclei (Fig. 13.13, C). They store food materials and are irregular in shape.

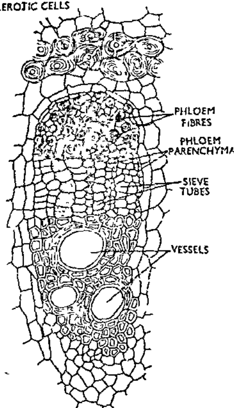


Fig. 13.11. *Gnetum ula* A vascular bundle showing phloem and xylem (*After Maheshwary* and *Vasil*).

In *Gnetum* the sieve-tubes are arranged in distinct rows (Fig. 13.11) and the phloem parenchyma in the angles between them (Fig. 13.11). They look like companion cells of the angiosperms, but Thompson (1919) pointed out the difference between the development of companion cells in the angiosperms and the formation of phloem parenchyma in *Gnetum*. In the angiosperms, the companion cells and sieve-tubes develop from the same mother cell, which is not the case in *Gnetum*. In *Gnetum gnemonoides*, the phloem of the seedling stem is devoid of parenchyma cells. Phloem fibres are abundant in *G. ula* (Fig. 13.11).

The secondary xylem is com- [illegible] ...12). The secondary wood in *Gnetum* is characterised by the presence of vessels with a single row of perforations at their end walls. In *G. paniculatum*, the vessels have two rows of perforations at their end walls. In *G. africanum*, Duthie (1912) observed various stages leading from a

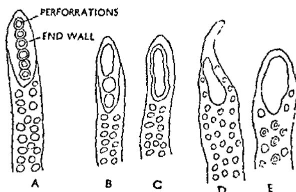


Fig. 13.12. *Gnetum africanum* (A—E). Showing perforations in the end walls of vessels. (*After Duthie*)

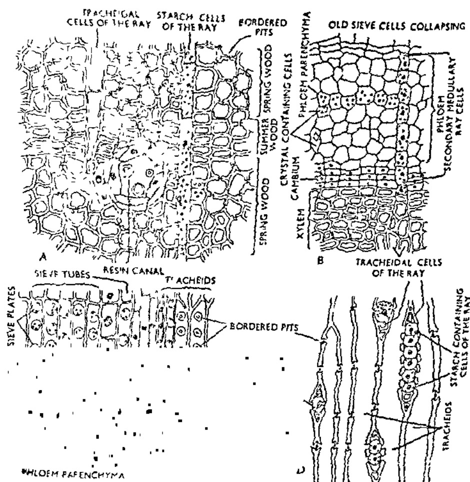


Fig. 13.13. *Pinus* (A—D) A, T.S. through wood of Pinus showing spring wood, boundary of years growth and summer wood. Resin canals and medullary rays are also shown. B, T.S. through the outer margin of the secondary xylem showing portion of phloem also C, Radial longitudinal section through phloem and xylem showing the various kinds of cells composing a secondary medullary ray. D, L S. through secondary xylem showing rays and tracheids.

row of perforations (Fig. 13.12, A) to the formation of a single, long and narrow or even rounded perforation at the end walls of vessels (Fig. 13.12, A—E). In other gymnosperms, tracheids are the characteristic conducting elements. They vary in length from 0·5—5 mm. and are usually arranged in radial rows. Their radial arrangement is due to the fact that tracheids grow almost in a radial direction and only rarely in a horizontal direction. Longitudinal growth is also slight. The pits are present in radial walls. They possess bordered pits, that have an oval or a more or less circular shape. Xylem fibres are also present. Xylem parenchyma is found in smaller amounts. Secondary xylem of gymnosperms also contains resin ducts that are lined with epithelial cells which later on project into the cavity of the resin ducts and appear like tyloses. Actually, it differs from the tyloses.

During tylosis the neighbouring xylem parenchyma cells protrude into the cavities of the conducting elements, whereas, in this case, the cells lining the cavities protrude and block them. Such structures have been designated as **tylosoids.** In *Picea*, *Pinus* and *Larix*, the wood parenchyma is restricted solely around the resin ducts. In some conifers, simple columns of wood parenchyma occur in-between the tracheids. In *Taxus*, wood parenchyma is completely absent.

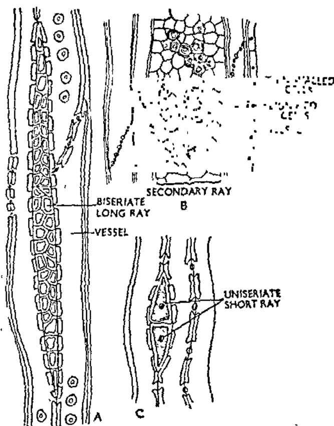


Fig. 13.14. *Gnetum ula*. Medullary rays. A, Tangential longitudinal section of a part of stem showing a long biseriate ray. B, Multiseriate ray showing thin-walled and thick-walled cells. C, uniseriate and short ray. (*After Maheshwari and Vasil*).

The secondary medullary rays in the secondary xylem of *Pinus* consist of two kinds of cells *viz.*, the tracheidal cells and the ordinary parenchyma cells. The tracheidal cells or the ray tracheids posses lignified walls with bordered pits (Fig. 13 13, C). The rays serve to transport the assimilation products formed in the leaves and flowing downwards in the phloem in a radial direction into wood of the stem and the roots. In the opposite direction they conduct water away from the wood. The rays penetrate equally into the xylem and the phloem (
of these func
of consideral

13.14, C), biseriate (Fig. 13.14, A) or multiseriate (Fig. 13.14, B). Shorter rays also occur (Fig. 13.14, C ; 13.13, D). In *Gnetum* (Fig. 13.14, A,C), the multiseriate rays have both parenchyma cells and thick-walled lignified cells (Fig. 13.14, B). Pearson (1929) reported the presence of xylem and phloem elements in the ray tissues of multiseriate rays of *Gnetum*, thus indicating their compound structure.

Formation of annual rings is similar to the dicots. In Gymnosperms the tracheids in spring wood have broader lumina and those in summer wood have narrow lumina. Within an annual ring the transition from the broad to narrow elements is gradual, but that from narrow to broad of the next ring is abrupt thus making a sharp boundary between the two rings.

SECONDARY GROWTH IN THE MONOCOTYLEDONS

Generally, the vascular bundles in the monocots are closed [illegible] growth takes [illegible] activity of a [illegible] ctivity of the [illegible] the primary [illegible] thick zone of [illegible] develops only in that region of the stem which has stopped elongating. The shape of these cells may be rectangular, fusiform or with one flat end and the other narrow and pointed end.

The cells of the cambium [illegible] off only a few cells towards [illegible] larger number towards the in[illegible] cells cut off towards the outer [illegible] those cut off towards the inne[illegible] and partly into secondary vascular bundles (Fig. 13.16). The inner parenchymatous cells are called the conjunctive tissue.

Develpment of the vascular bundles from cambial initials follows the following course. They develop from a single cell which is cut off from the cambial initial. This cell is centre of the vascular bundle. It divides first by anticlinal walls to form a row of two or three cells. These cells undergo periclinal divisions (Fig. 13.16) and then the divisions are irregular. The peripheral cells develop into xylem elements whereas the central cells differentiate into phloem elements. This leads to the formation of a concentric vascular bundle (Figs. 13.15, and 13.16). They are more or less oval in shape and are amphivasal. In *Kingia*, the xylem is U-shaped *i.e.*, it surrounds the phloem only on three sides. The xylem consists only of tracheids and xylem parenchyma. Vessels have not been reported in any of the species studied so far. Each bundle may be surrounded by a thin-walled or a thick-walled sheath. In *Xanthorrhoea*, the parenchyma cells, cut off towords the outer side of the cambium, secrete lot of resin. This leads to the formation

of resin sheath around the vascular region. This plant is a native of Australia and its wood is burnt by the natives (aborigines) on account of the beautiful flames that develop due to the burning of resin.

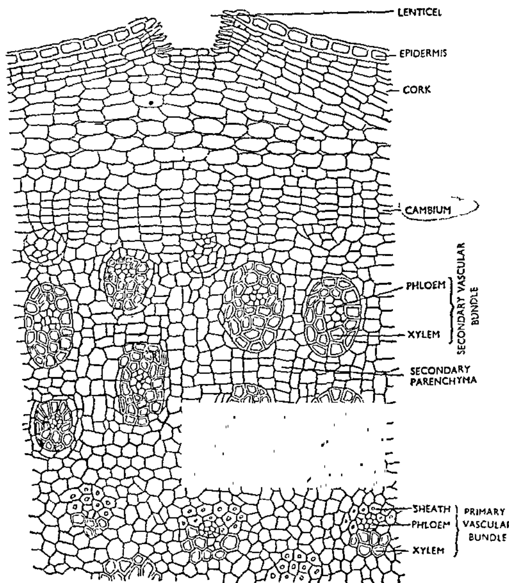


Fig. 13.15. T.S portion of a stem of *Dracaena* (Monocot), showing secondary growth.

In *Yucca brevifolia*, the cells of the pericycle become meristematic and function as cambium. Formation of periderm has also been reported in these monocots.

In some monocots the thickening of the stem takes place by a special meristem known as **Primary thickening meristem**. It has been reported in palms, rhizomes of *Musa* sp. and bulbs of *Tulipa* and

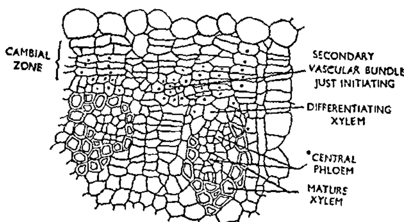


Fig. 13.16 *Dracaena* A part of the T S through stem enlarged to show the formation of the vascular bundles

Galanthus nivalis by Skutch (1932), Ball (1941), and Clowes (1961). In majority of the palms (Ball, 1941), the **primary thickening meristem** develops in the embryo just below the primordia of the first leaf and the sheath. It is a flat zone of meristematic cells. In the seedling stage it becomes concave and appears conical in form. As the seedling grows the **primary thickening meristem** again becomes flattened and ultimately in the mature young plant it assumes a concave form. It

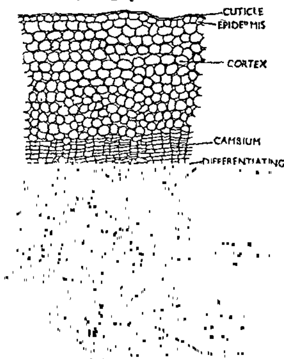


Fig. 13.17. *Aloe arborescens*. T.S. part of the stem showing secondary growth.

initiates from a group of cells just below the primordia of the first leaf and the sheath. These cells divide periclinally and form a meristematic layer called the **primary thickening meristem.** This meristem contributes both to the height and thickness of the stem. The procambial strands in the palms and corms of *Musa* sp. are derived mainly from this meristem. Only a few of them are derived from the shoot apex. The primary thickening meristem goes on forming the procambial strands which in turn give rise to the vascular bundles and thus add to the thickening of the stem.

Zodda (1940), Schoute (1942) and Tomlinson (1961) have reported another method of the thickening of stem in the palms. In some palms *e.g.*, *Roystonea*, the parenchymatous cells in the centre of the stem and the cells of the differentiated bundle sheath keep on dividing and expanding. The intercellular spaces also grow in size. This results in the increase in thickness. Tomlinson (1971) has termed such growth in thickness as **diffuse secondary growth.**

(*iii*) The vascular bundles may be present in the pith (medullary bundles).

(*iv*) The vascular bundles occur in the cortex (cortical bundles).

(*v*) Absence of vessels in the xylem

(*vi*) Presence of exclusive phloem and xylem bundles.

(*vii*) Polystelic condition.

(*viii*) Occurrence of internal vascular bundles

Scattered Vascular Bundles.

In some dicot stems the vascular bundles are not arranged in a ring

of vascu-

is of some

ctrum and

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and 14.3)

e.g., *Peperomia langsdorfii.*

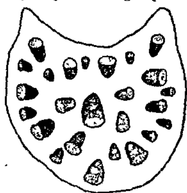


Fig. 14.1. T.S. (Diagrammatic) of petiole of *Anemone* showing scattered vascular bundles (dicot stem).

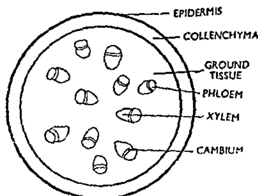


Fig. 14.2. T.S. (Diagrammatic) stem of *Peperomia langsdorfii* showing scattered vascular bundles.

Detailed internal structure of the stem *of Peperomia langsdorfii is* described below.

A transverse section (Fig. 14.2 and 14.3) reveals the following tissues :—

Epidermis. It is a single layer of compactly arranged and thin-walled rectangular cells. Cuticle is thin.

Cortex. It can be distinguished into an outer collenchymatous cortex and an inner parenchymatous cortex. Collenchyma forms a continuous and unbroken cylinder of 3 to 9 layers of cells in thickness. The inner cortex is parenchymatous and the cells enclose a large number of small, intercellular spaces. There is no distinct layer of *endodermis* and hence it is difficult to differentiate the inner thin-walled cortex from the pith. Pericycle is also absent.

Vascular region. In this species the vascular bundles are scattered and no definite outer ring of bundles is recognisable. These

scattered in the ground tissue as there is no distinction into pith and cortex due to the absence of pericycle and endodermis. The vascular bundles are conjoint, collateral, open and endarch.

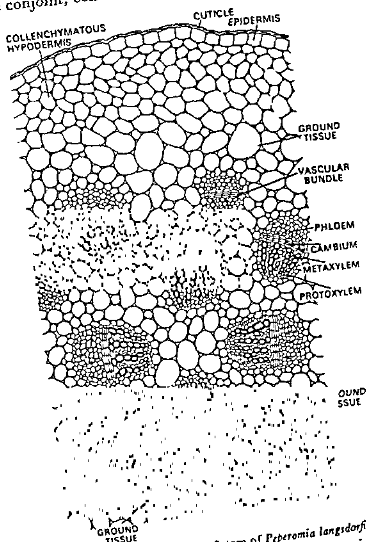


Fig. 14.3. T.S. portion of stem of *Peperomia langsdorfii*.

In *Peperomia berteroana*, there are two or three rings of vascular bundles which surround the central scattered vascular bundles. In *P. verticillata*, there are two concentric rings of 10—12 vascular bundles. In *P. deliculata*, there is a single ring of 4 vascular bundles. In *P. tenera*, there is only a single axile vascular strand. So there is a great variation in the vascular region of the genus *Peperomia*. Bundles can be said to be scattered only in *P. langsdorfii*.

Medullary Bundles

In many dicots, in addition to the normal ring of vascular bundles, there are present vascular bundles in the pith. The bundles in the

pith are called *medullary bundles* and may be scattered or arranged in definite circles or rings. The number of medullary bundles varies from one to many. These have been reported i

families. The common ones

Delphinium, *Glaucidium*, a

(*Amaranthus*, *Achyranthes*),

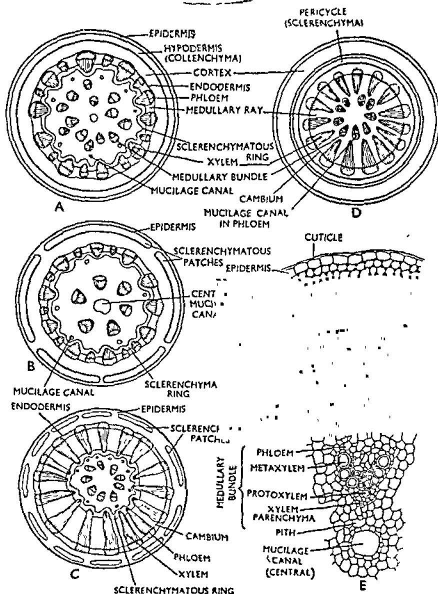


Fig. 14.4. Anatomy of the C
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bium do not produce xylem and phloem elements. The xylem groups are individually capped by sclerenchymatous patches towards their inner ends. The vessels have scalariform pits. Some of the vessels have tapering ends.

The medullary bundles are a few and arranged in a ring. The characteristic feature of the medullary bundles is the presence of a mucilage canal in the phloem.

4. *Piper excelsum* (Fig. 14.4 C). It differs from *P. jaborandi* in (*a*) possessing a sinuous sclerenchymatous zone internal to the outer ring of vascular bundles, (*b*) absence of sclerenchymatous pericycle, (*c*) presence of peripheral mucilage canals, and (*d*) absence of mucilage canals in the phloem of medullary bundles. It resembles *P. juborandi* in (*a*) possessing radially elongated xylem groups in the outer ring of vascular bundles, (*b*) the medullary bundles are arranged in a ring and (*c*) presence of a complete ring of cambium.

5. *Piper fluminense.* In this species the vascular bundles in the peripheral ring are much smaller and are separated from the scattered medullary bundles by a sclerenchymatous zone.

6. *Piper methysticum.* It is similar to *Piper betle.* Interfascicular cambium develops late and cuts off cells only towards the inner side. Hoffstad (1916) described the course of vascular bundles in this species. According to him, the foliar bundles after entering the stem remain peripheral in their course in the first internode, but become medullary in two lower internodes. The stem increases in thickness by the activity of the cambium as well as by the proliferation of cells in the pith.

Mirabilis jalapa (Nyctaginaceae). In a primary state, a transverse section through the stem of *Mirabilis jalapa* reveals the following tissues (Fig. 14.5) :—

Epidermis. It consists of a single layer of thin-walled and compactly arranged cells covered with cuticle.

Cortex. It consists of sub-epidermal collenchyma followed by chlorenchyma (fig. 14.5). The collenchyma occurs in the form of patches below the epidermis. It forms two to four layers of cells thickened at the corners. Next to it the chlorenchyma is composed of a few layers of loosely arranged oval or spherical cells that enclose small intercellular spaces.

Endodermis. It is not clearly demarcated and can be made out due to its cells being colourless and full of starch. Fresh sections stained with iodine stain the starch grains blue and bring out the identity of this layer.

Pericycle. It consists of one or two layers of thin-walled cells.

Primary Vascular System. It consists of a normal ring of vascular bundles next to pith and numerous scattered bundles in the pith. These are called medullary bundles. Maheshwari (1930) reports the presence of incomplete dwarf bundles in the outer ring. These contain only phloem. Their development is due to centripetal development

Cactaceae (*Trichocereus candicans*, *Echinocactus*, *Echinopsis*, etc.), Cruciferae (*Raphanus sativus*, [illegible] (*P*[illegible] *menidala*), *Chenopodiaceae* (*Ch*[illegible] *gaincillea*, *Boerhaavia*), *Mal*[illegible] (*Apium graveolens*, *Ferula*, [illegible]

A detailed internal structure of some of the important genera, showing medullary bundles is given below.

Anatomy of the Genus Piper (Piperaceae)

There is great variation in the internal set-up of the tissues in the genus *Piper*. The following distinct types can be recognised :

1. *Piper betle* (Fig. 14.4 A, E) :—In this case, there is single-layered epidermis composed of thin-walled and compactly arranged cells. It is followe[illegible] w layers of parenc[illegible] lls of the cortex [illegible] cortex is *endodermis*. *It is distinct and is made up of a single layer of* barrel-shaped cells. There is no pericycle.

Next to the endodermis there is the outer ring of vascular bundles. This ring is separated from the pith by a sinuous zone of sclerenchyma (Fig. 14.4 A, E). Each vascular bundle of the outer ring is conjoint, collateral and endarch. The xylem vessels are arranged in U-shaped groups (Fig. 14.4 E). The end-walls of the vessels have simple perforations. Vessels have simple pits. Xylem parenchyma is paratracheal. Xylem fibres both simple and septate have been reported. They have simple pits along their tangential and radial walls. The phloem has sieve tubes, companion cells, phloem parenchyma and phloem fibres. The phloem fibres form sclerenchyma groups capping each vascular bundle in the outer ring.

There are numerous medullary bundles that lie scattered in the pith. These bundles grow in thickness to a limited extent. There is one large mucilage canal (Fig. 14.4 A, E) in the centre of the pith and *11—12 small mucilage canals in the periphery of the pith*. The medullary bundles are separated from the outer ring by a sinuous sclerenchymatous zone.

bium do not produce xylem and phloem elements. The xylem groups are individually capped by sclerenchymatous patches towards their inner ends. The vessels have scalariform pits. Some of the vessels have tapering ends.

The medullary bundles are a few and arranged in a ring. The characteristic feature of the medullary bundles is the presence of a mucilage canal in the phloem.

4. *Piper excelsum* (Fig. 14.4 C). It differs from *P. jaborandi* in (*a*) possessing a sinuous sclerenchymatous zone internal to the outer ring of vascular bundles, (*b*) absence of sclerenchymatous pericycle, (*c*) presence of peripheral mucilage canals, and (*d*) absence of mucilage canals in the phloem of medullary bundles. It resembles *P. juborandi* in (*a*) possessing radially elongated xylem groups in the outer ring of vascular bundles, (*b*) the medullary bundles are arranged in a ring and (*c*) presence of a complete ring of cambium.

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6. *Piper methysticum.* It is similar to *Piper betle.* Interfascicular cambium develops late and cuts off cells only towards the inner side. Hoffstad (1916) described the course of vascular bundles in this species. According to him, the foliar bundles after entering the stem remain peripheral in their course in the first internode, but become medullary in two lower internodes. The stem increases in thickness by the activity of the cambium as well as by the proliferation of cells in the pith.

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Cortex. It consists of sub-epidermal collenchyma followed by chlorenchyma (fig. 14.5). The collenchyma occurs in the form of patches below the epidermis. It forms two to four layers of cells thickened at the corners. Next to it the chlorenchyma is composed of a few layers of loosely arranged oval or spherical cells that enclose small intercellular spaces.

Endodermis. It is not clearly demarcated and can be made out due to its cells being colourless and full of starch. Fresh sections stained with iodine stain the starch grains blue and bring out the identity of this layer.

Pericycle. It consists of one or two layers of thin-walled cells.

Primary Vascular System. It consists of a normal ring of vascular bundles next to pith and numerous scattered bundles in the pith. These are called medullary bundles. Maheshwari (1930) reports the presence of incomplete dwarf bundles in the outer ring. These contain only phloem. Their development is due to centripetal development

of phloem elements from the procambial strands. The xylem elements which develop from inner procambial strands and proceed outwards (centrifugal) fail to develop, thus, resulting in the formation of phloem bundles. The complete bundles in the outer ring are conjoint, collateral, endarch and open. The phloem consists of sieve-tubes, companion cells and phloem parenchyma. Phloem fibres are absent. Xylem includes well-developed vessels with spiral thickening; simple, pitted and reticulate vessels are few (Metcalf and Chalk). These bundles are smaller in size and develop later than the medullary bundles

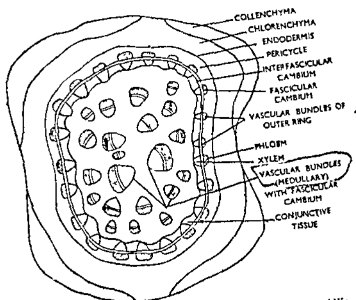


Fig. 14.5. T.S. (diagrammatic) stem of *Mirabilis jalapa*. Note the medullary vascular bundles with their own cambia.

Bougainvillea. (Figs. 14.7. and 14.8). It belongs to family *Nyctaginaceae*. The young stem has almost an oval outline in a cross-section. In a primary state of growth, the stem shows the following structure :

Epidermis. It consists of a single layer of compactly arranged thin-walled cells. Multicellular epidermal hair are numerous. The cells in the hair are squarish or rectangular and each hair has a spherical apical cell. The cells in the hair and epidermis are filled with a pinkish sap. A thick cuticle covers the entire epidermis.

Cortex. It consists of patches of collenchymatous cells below the epidermis. Collenchyma, in older stems, forms a continuous cylinder. Next to this are a few layers of chlorenchymatous cells. In the young stems, chlorenchyma extends between the collenchymatous patches. Intercellular spaces are present between the chlorenchymatous cells.

Endodermis. It forms a distinct layer of barrel-shaped cells. The cells contain starch grains.

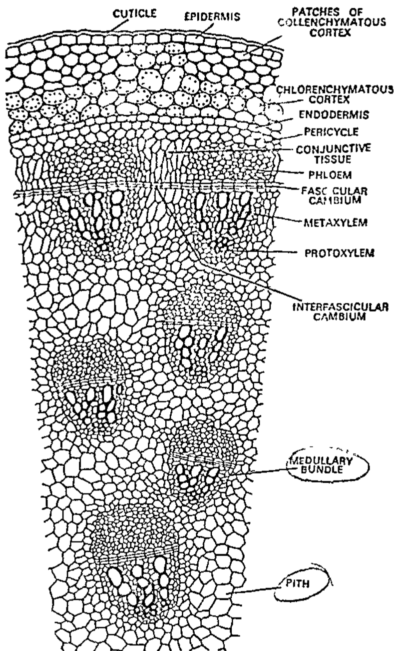


Fig 14 6 *Mirabilis Jalapa.* T.S. portion in detail, of stem, showing primary structure. Note the medullary bundles

Pericycle. It consists of one or two layers of parenchymatous cells.

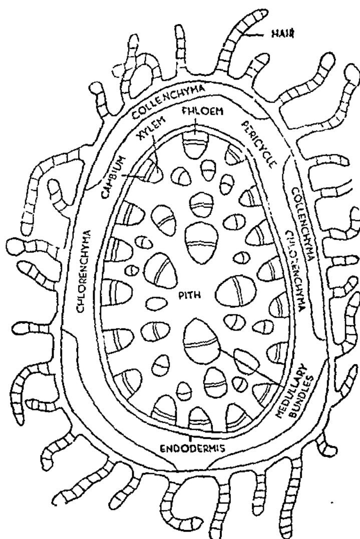


Fig. 14.7. T.S. (Diagrammatic) stem of *Bougainvillea*. Note the medullary bundles. The central ones have cambium.

Vascular System. In addition to the normal ring of conjoint, collateral, endarch and open bundles, there are numerous medullary bundles embedded in the pith (Figs. 14.7 and 14.8). The bundles in the outer ring are open and are discrete with broad medullary rays between them. The phloem consists of sieve-tubes, companion cells and phloem parenchyma. Phloem fibres are absent. The xylem has pitted, spiral and annular vessels. They are endarch *i.e.*, metaxylem is towa s the phloem and protoxylem towards the pith. Xylem parencl d tracheids are also present in the primary xylem. No ir cambia differentiate between adjacent vascular bundles ing.

The medullary bundles consist of four large b *tre of* the pith. They are conjoint, collateral, endarch . ow

in thickness to a limited extent by the activity of the fascicular cambium. These are surrounded by numerous scatterrd medullary bundles of a smaller size. Leaf trace bundles are also included. They lack cambium and are closed. Parenchymatous sheaths are also visible around the medullary bundles.

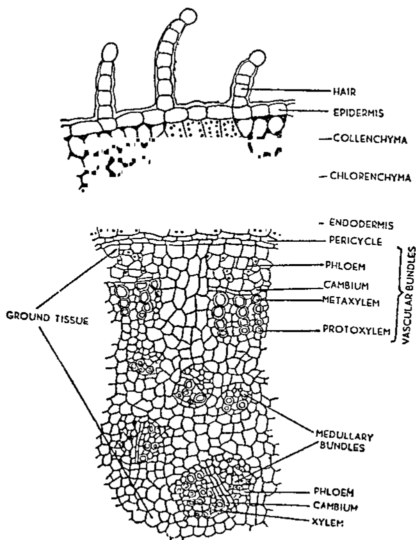


Fig. 14 8. T.S. (portion in detail) of stem of *Bougainvillea* showing primary structure.

In *Bougainvillea spectabillis*, there are 12—14 vascular bundles in the outer ring in a very young stem and about 6—10 in the pith. This number is calculated from young seedlings that are about 33 days old. The number is maximum in the *nodes* and minimum in the ... The med... with ...

anastomose in the internode either with each other or with medullary bundles. At the cotyledonary node the vascular bundles of the outer ring anastomose with the medullary bundles (Stevenson and Popham, (1973). Same is the case in the petioles. The outer ring of vascular bundles differentiates from a complete ring of procambial strands.

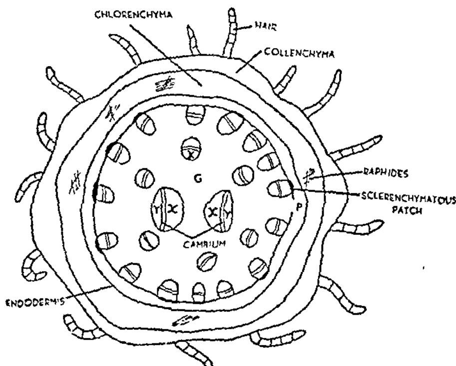


Fig. 14.9. T.S. (diagrammatic) stem of *Boerhaavia diffusa*, showing medullary bundles. X=xylem : Y=phloem

Pith or Ground Tissue. It is made up of parenchymatous cells which have intercellular spaces.

Boerhaavia d ... omy of *Boerhaavia diffusa* was studied in det ... 42—61). A cross-section of the young stem ... wavy outline and shows the following arrangement of the primary tissues :—

Epidermis. It is made up of a single layer of compactly arranged cells with lateral and outer walls thickened. The cells are filled with a violet sap. Cuticle is thick. Large numbers of multicellular hair arise from the epidermis.

Cortex. It consists of collenchyma and chlorenchyma. The former forms 3 to 4 layers below the epidermis. At certain places, it is less developed and is represented by a single layer of cells. The cells contain a few chloroplasts in the young stems. The chlorenchyma forms 4 to 6 layers below the collenchyma. Its cells are thin-walled, circular, oval or even polygonal and are full of chloroplasts. They enclose small intercellular spaces. Raphides or needle-shaped crystals of calcium carbonate are also present in the cortex (Fig. 14.9).

Endodermis. It is clearly defined and consists of thick-walled tubular cells.

Pericycle. It is parenchymatous with small isolated patches of sclerenchymatous fibres. In the specimens collected from Punjab, the sclerenchymatous patches were not observed in the young stems.

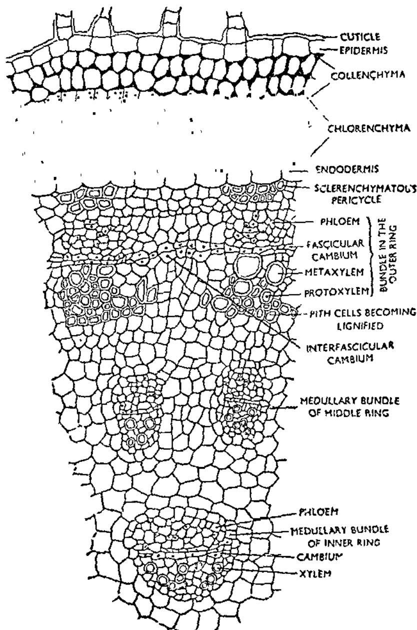


Fig. 14.10. T.S. (portion in detail) of stem of *Boerhaavia diffusa* showing medullary bundles and formation of first ring of cambium.

Vascular System. There are two large vascular bundles in the pith (Fig. 14.9). These are medullary bundles which are the largest in size and oval in shape. They are fully developed. These two bundles are surrounded by a middle ring of 6-14 vascular bundles. These bundles are smaller in size and oval or rounded in shape. These are in turn surrounded by an outer ring of 15-20 or more small vascular bundles. The central bundles are enveloped in a thin-walled sheath and lie opposite to each other with phloem facing outwards and xylem towards the centre. They are *conjoint*, *collateral*, *endarch* and *open*. The phloem possesses sieve-tubes, companion cells and phloem parenchyma. Phloem fibres are absent. The xylem consists of vessels, tracheids and xylem parenchyma. The central large bundles increase in thickness to a limited extent by the activity of the fascicular cambium. The bundles in the middle ring are also conjoint, collateral, endarch and open and increase in thickness to a limited extent by the activity of the fascicular cambium. They are also enveloped within parenchymatous sheaths. The bundles in the outermost ring are small in size and are open, endarch, collateral and conjoint. The metaxylem vessels have simple pits in their walls. Reticulate vessels are also present. The protoxylem vessels have spiral and annular thickenings.

Amaranthus (Amaranthaceae). The various species of *Amaranthus* have received a great deal of attention from the botanists due to anomalous secondary growth and because of having extra-vascular bundles in the pith or medulla. A transverse section of the stem (Fig. 14.11) shows a number of shallow ridges and furrows and reveals the following tissues :

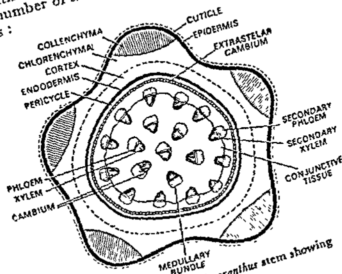


Fig. 14.11. T S. (diagrammatic) of *Amaranthus* stem showing medullary bundles and extrastelar cambium.

Primary structure (Fig. 14.11).

Epidermis. It consists of a single layer of slightly thick-walledcell s. There is a thick cuticle on the outer side. The inner and the lateral

walls of the cells are thin.

Cortex. Below the epidermis there are alternating groups of collen-

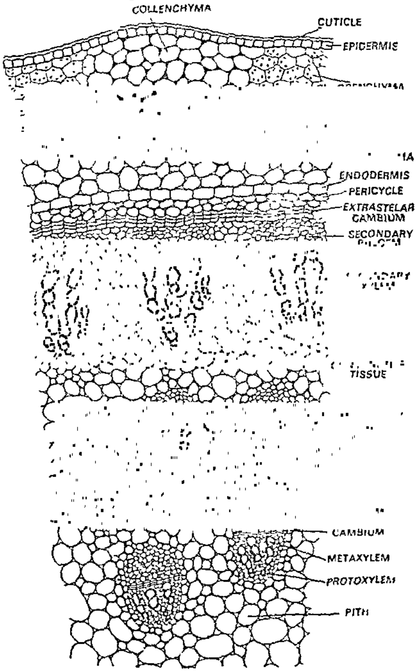


Fig. 14.12. *Amaranthus.* T.S. portion of stem showing detailed internal structure. Note the medullary bundles. The extrastelar cambium has also appeared and secondary tissues have started developing.

chymatous and chlorenchymatous cells (Fig. 14.12). Sometimes, the chlorenchymatous layers enclose the collenchymatous groups on either side and below. Next to this is a narrow zone of thin-walled cortex. It consists of loosely arranged parenchymatous cells.

Endodermis. It is not very distinct, but the cells are small and elongated. They lack casparian strips.

Pericycle. It is composed of a few layers of compactly arranged thin-walled cells. The cells are small and have small intercellular spaces.

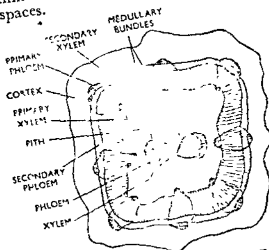


Fig 14.13 T.S. (Diagrammatic) stem of *Achyranthes aspera*, showing medullary bundles

Vascular system. There is a normal ring of discrete vascular bundles separated by wide regions of parenchyma, which constitute medullary rays. The bundles are conjoint, collateral, and open. The phloem is towards the outer side and consists of sieve-tubes, companion cells and phloem parenchyma. The cambium is distinct. The xylem consists of proto- and metaxylem vessels, and abundant xylem parenchyma.

The medullary bundles are scattered in the pith and are conjoint, collateral, endarch and open. The cambial activity in these bundles is short. The cambium soon becomes inactive. There is a distinct pith in the centre.

Stem of Achyranthes. Joshi (1931, 1934, 1951) described in detail the anatomy of *Achyranthes aspera*. Shrivastva (1960) described the anatomy of *A. aspera* var. *prophyristachya* and *A. coynei* (1962). The account here refers to *A. aspera* (Figs. 14.13 and 14.14). A transverse section of the young stem (internodes) shows a number of ridges and furrows. The following tissues are seen :—

Epidermis. It is composed of a single layer of tubular cells. The cells are compactly arranged with their outer and lateral walls slightly thickened and lignified. It is covered by a thick cuticle. Epidermal hair are long and multicellular.

Cortex. Below the ridges, there is well-developed collenchyma. A few layers of chlorenchymatous cells are found below the furrows. Next to this is the parenchymatous cortex. It is composed of two or three layers of parenchymatous cells. They have few intercellular spaces.

Endodermis. It is distinct and consists of a single layer of parenchymatous cells. The cells are elongated.

Pericycle. It consists of sclerenchymatous and parenchymatous patches of cells.

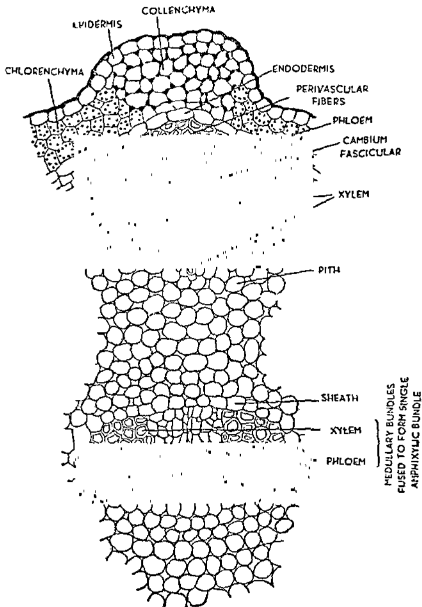


Fig. 14.14 *Achyranthes aspera*. T.S of a portion of stem showing detailed internal structure. Note the fused medullary vascular bundles.

Vascular System In the young stem (showing primary structure) there is present a normal ring of vascular bundles. The bundles are small and are separated by wide medullary rays. There is distinct cambial strip between the phloem and the xylem. The xylem contists of vessels, tracheids, parenchyma, and fibres. In the phloem, phloem fibres are absent in *A. aspera*. Sieve tubes, companion cells, and parenchyma are present. In *A. coynei*, phloem possesses phloem fibres.



Fig. 14.15. *Achyranthes aspera.* Photomicrograph of a T.S. through stem showing two separate medullary bundles

In addition to the normal ring of vascular bundles, there are present two medullary bundles. In *A. aspera,* these bundles fuse together and form a single amphixylic vascular bundle (phloem in the centre and xylem on its either side). Such a fusion is very clear in plants collected from Panjab (Fig. 14.13). The medullary bundles are opposite to each other and are well-developed. They are conjoint, collateral, endarch and closed and are enclosed in a parenchymatous sheath.

In *A. aspera* var. *porphyristachya,* Shrivastva (1960) described that these medullary vascular bundles are free in the upper 4 or 5 internodes in the flowering axis. Lower down, they unite with each other to form a double or amphixylic vascular bundle. The medullary vascular bundles in *A. bidentata, A. argentea, A. crispa* and *A. coynei* are free and do not

unite. Joshi (1931, 1934) observed that, in *A. aspera*, two separate medullary bundles occur throughout the length of the internode only in the region below the inflorescence. In the lower portions of shoot they are free only in regions immediately above or below the node and are fused throughout the rest of the internodes. Dastur (1925) observed two separate medullary bundles in the internode throughout the entire plant. Only 20% of the plants from Bombay showed fused medullary bundles, the rest had free medullary bundles. From Calcutta the plants of *A. aspera* showed fused medullary bundles only in one specimen. In Benaras, 5% plants showed fused medullary bundles. So



Fig. [illegible]

There is a great variety [illegible] *A. aspera*. Joshi (1931) [illegible]

[illegible]

different parts of India led Joshi to conclude that *A. aspera* originated in tropical region and then spread to cooler parts. Joshi (1951) regarded the occurrence of free medullary bundles throughout the internode as a primitive condition, and their fusion in the middle of the internode to form a single strand is a derived condi-

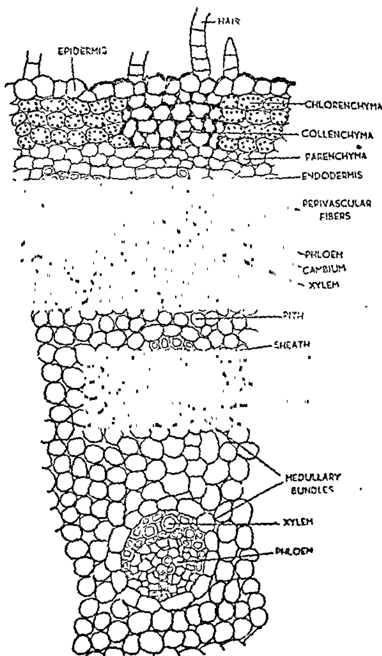


Fig. 14.17. T. S. portion of stem of *Achyranthes coynei*, showing two separate medullary bundles. (*After Shrivastva*).

tion. Gupta (1934) described that in *A. aspera* of the two medullary vascular bundles one is normal and the other is amphicribral. The cells in the pith and the cortex show crystals of calcium carbonate.

In *A. coysei* Fig. 14.17 Shrivastava (1962) described 4 medullary bundles in the pith (Fig. 14.18 A,C) which are circular or oval in shape and are present in the 4 corners of the inflorescence axis. They are surrounded by a parenchymatous sheath. These bundles contain phloem fibres. As the axis matures, the two vascular bundles lying opposite to each other at the broader sides fuse together laterally (Fig. 14.18, B). Now there are two medullary bundles. This happens in the first internode below the inflorescence axis. They are situated opposite to each other and are oval or circular in outline. They remain separate and never fuse with each other. In this species, the medullary bundles appear at the tip of the axis before the development of the normal bundles. The xylem in the medullary bundles is U-shaped (Fig. 14.18, C).

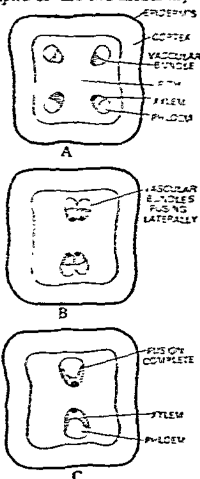


Fig. 14.18. A—C. Diagrammatic representation of the fusion of the medullary bundles in *Achyranthes coynei*. A, four bundles in pith. B, They fuse laterally. C, Fusion complete. (*After Shrivastava, 1962*).

Collenchyma, chlorenchyma and sclerenchymatous patches of pericycle are the xerophytic characteristic.

Inversely oriented medullary bundles have been reported in some members of Araliaceae (*Aralia racemosa*, *Ereutherococcus*, *Actinophyllum*). In *Kissodendron* and *Didymopanax*, the medullary bundles are variously oriented.

In some members of Araliaceae *Brassaiopsis hainla* and *Boerlagiodendron*, the stems possess both cortical and medullary bundles. Such examples are also found in Melastomaceae.

CORTICAL BUNDLES

In addition to the normal ring of vascular bundles some dicots possess bundles in the cortex also. These bundles are called cortical bundles. Metcalfe and Chalk (vol. 2, p 1342) list thirty-eight families in which cortical bundles have been reported. Some important ones are: *Oleaceae* (*Nyctanthes arbor-tristis*), *Calycanthaceae* (*Calycanthus*), *Casuarinaceae* (*Casuarina*), *Umbelliferae*, (*Eryngium*, *Mulinum*, *Seler trilobum*) *Papilionaceae* (*Lathyrus sylvestris*, *L. maritimus*, *Orobus*, etc), *Rutaceae*

different parts of India led Joshi to conclude that *A. aspera* originated in tropical region and then spread to cooler parts. Joshi (1951) regarded the occurrence of free medullary bundles throughout the internode as a primitive condition, and their fusion in the middle of the internode to form a single strand is a derived condi-

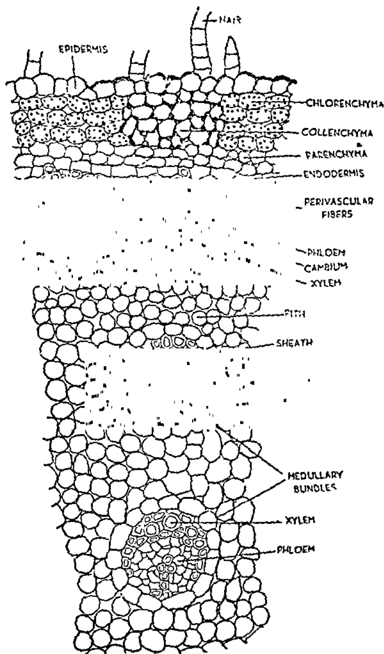


Fig. 14 17. T. S. portion of stem of *Achyranthes coynei*, showing two separate medullary bundles. (*After Shrivastva*).

tion. Gupta (1934) described that in *A. aspera* of the two medullary vascular bundles one is normal and the other is amphixylic. The cells in the pith and the cortex show crystals of calcium carbonate.

In *A. coynei* (Fig. 14.17) Shrivastva (1962) described 4 medullary bundles in the pith (Fig. 14.18 A,C) which are circular or oval in shape and are present in the 4 corners of the inflorescence axis. They are surrounded by a parenchymatous sheath. These bundles contain phloem fibres. As the axis matures, the two vascular bundles lying opposite to each other at the broader sides fuse together laterally (Fig. 14 18, B). Now there are two meduallary bundles. This happens in the first internode below the infloresc-ence axis They are situated opposite to each other and are oval or circular in outline. They remain separate and never fuse with each other. In this species, the medullary bundles appear at the tip of the axis before the development of the normal bundles. The xylem in the medullary bundles is U-shaped (Fig. 14.18. C).

Collenchyma, chlorenchyma and sclerenchymatous patches of pericycle are the xerophytic characteristic.

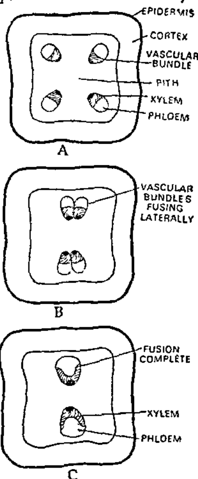


Fig. 14.18. A—C. Diagrammatic representation of the fusion of the medullary bundles in *Achyranthes coynei*. A, four bundles in pith. B, They fuse laterally. C, Fusion complete. (*After Shrivastva, 1962*).

Inversely oriented medullary bundles have been reported in some members of Araliaceae (*Aralia racemosa*, *Erenopanax*, *Arthrophyllum*). In *Kissodendron* and *Didymopanax*, the medullary bundles are variously oriented.

In some members of Araliaceae (*Brassiopsis tupidanthus* and *Boerlogiodendron*), the stems possess both cortical and medullary bundles. Such examples are also found in Melastomaceae.

CORTICAL BUNDLES

In addition to the normal ring of vascular bundles some dicots
[illegible] These bundles are called cortical
[illegible] p 1342) list thirty-eight families in
[illegible] reported. Some important ones
[illegible] *is*), *Calycanthaceae* (*Calycanthus*),
[illegible] (*Eryngium*, *Mulinum*, *Siler trilobum*)
[illegible]*apiuonaiae* (*Lathyrus sylvestris*, *L. maritimus*, *Borbonia*, etc), *Rutaceae*

(*Eriostemon, Pilocarpus*), *Melastomaceae* (in about 18 genera).

Nyctanthes arbortristis (Oleaceae) :—A transverse section (Fig. 14.19 A, B) reveals a squarish outline. The stem has four prominent angles and reveals the following structure.

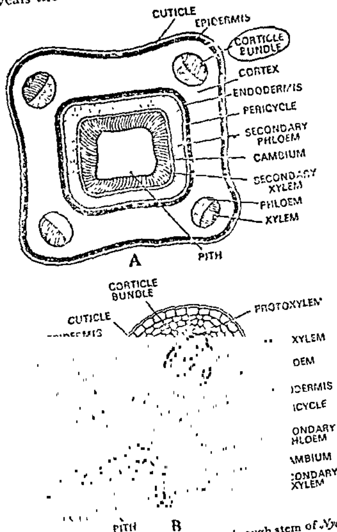


Fig. 14.19. A. diagrammatic T.S. through stem of *Nyctanthes arbortristis* showing cortical bundles B. A portion in detail. Note the orientation of the cortical bundles the phloem facing inwards and the xylem outwards.

Epidermis. It is a single layer of parenchymatous cells. The cells are compactly arranged and covered by an uninterrupted thick cuticle. Multicellular hair also arise from the epidermis.

Cortex. It is parenchymatous. The cells enclose small intercellular spaces. The endodermis is indistinguishable.

Vascular Region. There is a normal ring of vascular bundles that are open, endarch, conjoint and collateral. In addition to this normal

ring, there are present four vascular bundles in the cortex. These cortical bundles are restricted to the prominent angles of the stem. These cortical bundles are inversely oriented *i.e.*, their phloem is towards the inner side and xylem pointed towards the epidermis.

In the centre there is broad pith which is composed of thin-walled cells.

In *Calycanthus* and *Casuarina*, the cortical bundles are not oriented and have their phloem towards the epidermis and xylem towards the inner side.

In some members of the family *Crassulaceae* (*Aeonium, Greenovia Rochea* and *Kalanchoe*), the cortical bundles are concentric with xylem in the centre and completely surrounded by phloem.

In *Rhipsalis crispata* (Cactaceae), Solereder reported two rows of cortical bundles in the angles In *Hatiora salicornioides* and in a number of species of *Rhipsalis* (*R. cassutha, R cribrata, R flaccosa* etc.) the cortical bundles are arranged in small circular groups. The vascular bundles in the normal ring are discrete and separated by broad medullary rays in the primary state. They become continuous only during secondary growth.

In *Limonium vulgare* (Plumbaginaceae), the cortical vascular bundles are numerous and irregularly scattered all over the cortex.

In *Lobelia rhynchopetalum*, Hauman (1935) has reported a complex system of cortical bundles. The cortex in this species is fleshy.

NATURE OF MEDULLARY AND CORTICAL BUNDLES

Worsdell (1915, 1919) arrived at some general conclusions after studying the anatomy of Cucurbitaceae and Compositae. He applied them to all [illegible] According to him the [illegible] of bundles as is found in [illegible] tem of flowering plants, [illegible] and dicots have mostly [illegible] al phloem found in the stems of some families of the dicotyledons (Solanaceae, Cucurbitaceae, Convolvulaceae) is the last vestige of this ancestral condition. Most of Worsdell's evidence is drawn from a study of the petioles and the flowering peduncles which are regarded as conservative organs and are supposed to retain the ancestral structure—medullary bundles or a scattered disposition of the bundles—more or less well preserved when it has become extinct or almost so in the stem.

Joshi (1932) while commenting upon Worsdell's view states, "Worsdell did not use the evidence from the anatomy of *Heptapleurum* or any other Arali[illegible]
easily utilised it. [illegible]
the stem but these [illegible]
petiole. Similar c[illegible]
Araliaceae. *Aralia spinosa* possesses a ring of inversely oriented ring of medullary bundles in the petiole, while these are absent from the stem though found in the stem of several other species of *Aralia* and

Endodermis. It is distinct as a last layer of the cortex. The barrel-shaped cells are compactly arranged and contain starch grains.

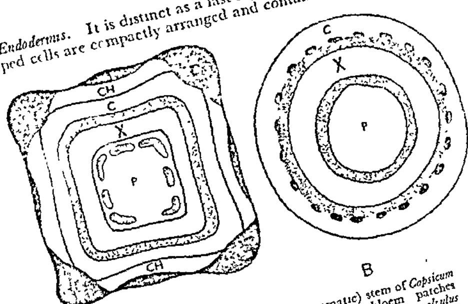


Fig. 14.21. A—B. A. T.S. (diagrammatic) stem of *Capsicum annuum* showing internal or intraxylary phloem patches (stippled patches next to xylem). B. T.S. stem of *Convolvulus floridus* showing complete ring of internal phloem (Stippled part next to xylem). C—cortex : X—xylem ; P—pith. CH—chlorenchyma.

Pericycle. It is parenchymatous and consists of a few layers of cells.

Vascular Region. In the primary state the stem consists of a ring of conjoint, collateral, endarch and open vascular bundles. Distinct patches of internal phloem are present next to the vascular bundles. These are embedded in the peripheral region of the pith. Phloem consists of only sieve-tubes, companion cells and phloem parenchyma. The internal phloem is also primary in origin.

Pith. It occupies the centre of the stem and consists of thin-walled cells with intercellular spaces between them.

Secondary growth begins with the formation of complete cambial ring, which cuts off secondary phloem towards ... ter side and secondary xylem towards the inner side. Phloem ... absent in the phloem and it is in the form ... ntinuous ... the outerside of the xylem. The sec... m ring ... here and there by secondary medulla ... sists ... trach~ids and xylem parenchyma ...

Epidermis. It consists of a single layer of thin-walled cells. The cells are compactly arranged and are covered by thick layer of cuticle.

Cortex. The cortex can be distinguished into hypodermis, chlorenchymatous cortex and endodermis. The hypodermis is composed of a single layer of thin-walled cells lying immediately below the epidermis. The chlorenchymatous cortex is made up of four to five layers of thin-walled cells. The cells contain abundant chloroplasts and are loosely arranged. The last layer of cortex is devoid of chloroplasts and is made up of barrel-shaped cells that are compactly arranged and contain starch grains.

Pericycle. It is made up of several layers of compactly arranged cells. Most of the pericycle is composed of thin-walled cells but patches of sclerenchymatous cells also occur in the broad parenchymatous zone.

Vascular region. In the primary state, there is a ring of discrete vascular bundles that are conjoint, bicollateral, open and endarch. The bundles are regarded as bicollateral because of the presence of internal phloem. At the commencement of secondary growth a complete cambial ring is formed cutting off cells towards inner and outer sides. Due to irregular activity of the cambium interxylary phloem patches are formed. Certain cells of cambium which normally produce secondary xylem elements start producing secondary phloem elements. The cells adjacent to these keep on producing secondary xylem elements. After some time these cambial cells again start producing secondary xylem instead of phloem elements. This leads to the formation of secondary phloem islands surrounded on all sides by secondary xylem. Such phloem patches are called interxylary phloem or included phloem.

Next to the pericycle is the normal ring of secondary phloem which consists of sieve-tubes, companion cells, and phloem parenchyma. Phloem fibres are absent. Primary phloem is also visible as small patches which later on get crushed.

Cambium. It consists of a single layer of thin-walled, actively dividing, brick-shaped cells. Sometimes, many layers of such cells are recognisable. These layers are due to the new cells cut off by the cambium ring and are in the process of developing into the vascular elements. These cells are similar in the earlier stages of development to the cambial cells and thus give the appearance of a many-layered cambium.

Xylem. The primary xylem consists of protoxylem and metaxylem vessels—the former towards the pith and the latter towards the cambium. Due to the secondary growth the primary xylem is visible as small patches towards the internal phloem. It consists of vessels, tracheids and xylem parenchyma. The secondary xylem occurs in the form of a continuous cylinder and consists of xylem vessels, tracheids, and xylem parenchyma. It is traversed by narrow secondary medullary rays. Patches of intraxylary or internal phloem are also present next to the xylem.

Pith. It is present in the centre and consists of parenchymatous cells, which have intercellular spaces between them.

Leptadaenia is an example of stem showing both interxylary and intraxylary phloem. The xerophytic characteristics of the stem are :— (*i*) presence of chlorenchyma ; (*ii*) thick cuticle : and (*iii*) patches of sclerenchyma.

Presence of Exclusive Phloem and Xylem Bundles

In some members of the family Ranunculaceae *e.g., Paeonia*, in addition to normal vascular bundles, there are also present exclusively xylem bundles. These bundles lack phloem.

In *Cuscuta*, in addition to normal collateral vascular bundles, there are also found exclusively phloem bundles. They occur between normal bundles and contain only phloem. Maheshwari (1930) noticed that in *Rumex crispus, Boerhaavia diffusa, Ricinus communis, Xanthium strumarum, Antigonon leptopus, Mirabilis Jalapa* and *Achyranthes aspera*, the normal ring of vascular bundles includes some incomplete dwarf bundles, which consist of only phloem. In such cases, there is only a centripetal development of phloem from the procambial cells, and xylem elements fail to develop centrifugally from inner side.

Absence of Vessels

Majority of the dicots possess vessels in the xylem and these are considered to be the main conducting channels for water. Their absence in some species is regarded as an anomalous feature. In these species, like the gymnosperms, tracheids are the main conducting channels. The vessels are absent in all the genera belonging to the families *Winteraceae* (*Drimys, Bubbia, Zygogynum, Exospermum, Pseudowintera, Belliolum*), *Trochodendraceae* (*Trochodendron*) and *Tetracentraceae* (*Tetracentron*) Vessels are absent in some aquatic angiosperms *e.g., Elodea canadensis, Utricularia, Ceratophyllum*, and *Hydrilla*.

Internal Vascular Bundles

These have been reported in some members of the family Polygonaceae (*Rumex crispus, R. orientalis, R. patientia*). Maheshwari (1929, pp. 89—117), Maheshwari and Balwant Singh (1942, pp. 113—7), and A.C. Joshi (1936, pp. 362—9) have studied in detail the anatomy of the genus *Rumex* in India. They have all reported the presence of internal bundles.

In R. *crispus* (Maheshwari, 1929), there is normal ring of vascular bundles. Each bundle is surrounded by a sclerenchymatous sheath. In addition to this normal ring, there is an inner ring of the vascular bundles. The vascular bundles of this inner ring are also surrounded by the same sheath which surrounds the vascular bundles of the outer ring. That is why the name *internal vascular bundles* had been given to them. These are not called medullary bundles because the bundles of the outer and inner rings are surrounded by common sclerenchymatous sheaths These internal bundles develop from the inner ends of the procambial strands which give rise to the normal ring of vascular bundles. They do not develop from the pith cells. The internal bundles contain only

phloem in the beginning. Later, each one of these phloem strands has a strip of cambium external to it. These cambial strips become active and produce secondary xylem externally and secondary phloem internally. The secondary phloem, therefore, lies above the primary phloem.

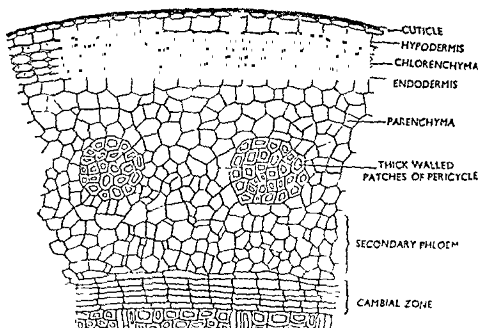


Fig. 14.22. T.S. part of stem of *Leptadenia* (Asclepiadaceae) showing interxylary or included phloem and internal or intraxylary phloem.

Later, the secondary xylem expands along the sides and completely surrounds the phloem. So the xylem in the internal bundles is wholly secondary in nature and phloem is partly primary and partly secondary. In *R crispus*, the internal bundles are absent in the basal region of the stem and are present in abundance near the apical regions. In *R. orientalis*, Joshi (1936) recorded them even in the basal parts of the stem. He also reported them in the hypocotyl of the seedlings of *R. orientalis*

(*b*) **Anomalous Monocot Stems.** Normal features of the monocots are that the vascular bundles are scattered and do not possess cambium. In *Tamus communis*, *Triticum*, *Hordeum*, *Oryza*, *Secale*, *Avena* and many other grasses, the vascular bundles are arranged in two or more definite rings This regular arrangement of vascular bundles in the monocots is considered to be a deviation from the normal scattered arrangement.

Stem of Tamus Communis (Dioscoreaceae). It is a monocot stem that exhibits a regular arrangement of the vascular bundles that are found in two rings (Fig. 14.23). A transverse section of the stem reveals the following structures .—

Epidermis. It consists of a single row of small cells, that are compactly arranged and are covered by a thin layer of cuticle.

Cortex. There is a well-defined cortex in *Tamus*. It consists of a few layers of oval or elliptical cells that are loosely arranged and enclose numerous intercellular spaces. Presence of a definite cortex in monocotyledonous stem is also an anomaly in itself especially when there is a well-defined endodermis and a pericycle.

Endodermis. It consists of a single layer of barrel-shaped cells.

Pericycle. It is composed of two or more layers of sclerenchymatous cells, that are uninterrupted and form a continuous cylinder around the central pith or ground tissue.

Vascular system. It consists of two rings of vascular bundles. They are not scattered and are arranged regularly in two rings, an anomalous feature for the monocots. The outer ring consists of smaller vascular bundles originating in the pericycle. The inner ring consists of larger bundles that are not surrounded by any sclerenchyma sheath. The bundles are collateral, endarch and closed. The xylem is in the form of 'V'. The metaxylem vessels occupy the arms of 'V' and are larger in size. Their walls have simple pits. The protoxylem occupies the vertex of the 'V' and has spiral and annualar thickenings. *Phloem* lacks phloem parenchyma and phloem fibres. It consists of only sieve-tubes and companion cells.

Pith. There is a distinct pith in the centre. It consists of rounded and thin-walled cells which enclose distinct intercellular spaces.

This stem resembles the monocots in possessing closed vascular bundles. It resembles dicots in possessing regular arrangement of vascular bundles, distinct cortex, endodermis, and pericycle.

The arrangement of medullary vascular bundles in the young stems of *Boerhaavia*, *Mirabilis* and *Amaranthus*, simulates the arrangement found

in the monocotyledons. Presence of a fascicular cambium is the only difference. Chamberlain (1921, pp. 293—304) and Barkley (1924, pp. 433—439) have described the growth rings in *Aloe* and *Yucca* respectively. These growth rings can be compared to a similar structure

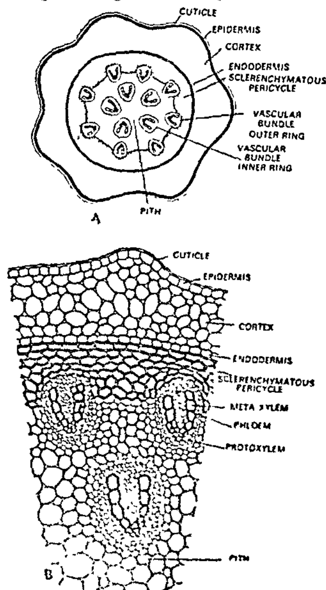


Fig. 14.23. Stem of *Tamus communis*. A. T.S. stem showing outline details. B. T.S. portion of stem showing detailed internal structure.

in the older stems of *B. diffusa*, *M. jalapa* and *Amaranthus*. Such a similarity has been pointed out by Maheswari (1930, p. 56). He has criticised Hutchinson for separating the family Nyctaginaceae from the families Amaranthaceae, Chenopodiaceae and others and putting it under a separate order, Thymelaeales. The close anatomical similarities

between these families go against such a separation. Maheshwari has also suggested. "The similarity of the centrospermales vascular anatomy to that of the monocots has never been given serious consideration by Botanists. The similarity between stems like those of *Boerhaavia*, *Mirabilis*, and *Amaranthus*, to monocot stems......Might it be that such plants represent in some way transition between the typical Dicot and Monocot stem organisation by a gradual weakening of cambial activity and scattering bundles ?" He has further remarked. "It can only be said that the centrospermales probably represent a distinct and a separate evolutionary line and that the similarity with the Monocots in the scattered arrangement of bundles may be something more than accidental."

We should also not lose sight of the fact that several grasses, including stems like *Tamus communis*, have an arrangement of vascular bundles like the dicots. In *Tamus* there is a distinct pith in the centre and clear demarcation between pith and the cortex. Such examples point out towards a close phylogenetic relationship between the two classes of angiosperms, but do not throw much light on the origin of one from the other. These anatomical resemblances between monocots and dicots go hand in hand with the resemblances in the male and the female gametophytes, endosperms and the process of fertilization. Regarding cotyledons there are some monocots with two cotyledons and some dicots with one cotyledon. Such resemblances were also pointed out by Maheshwari (1950) at a later stage.

The anomalous features in the monocot stem of *Tamus communis* can be listed as under :

(*i*) Presence of endodermis which delimits cortex from the vascular region and pith.

(*ii*) Presence of a distinct sclerenchymatous pericycle below the endodermis.

(*iii*) Vascular bundles arranged in definite rings.

The monocot features in the stem are :—

(*i*) Vascular bundles are closed and numerous.

(*ii*) Differentiation of vascular bundles in the pericycle.

(*iii*) Characteristic 'V'-like arrangement of xylem vessels.

(*iv*) Absence of phloem parenchyma.

Detailed structure of some members of the family Graminae, which show ring-like arrangement of vascular bundles has been discussed in chapter 12.

B. ANOMALOUS SECONDARY GROWTH

The normal procedure of secondary growth in the dicotyledons has been described in chapter 13. The secondary growth resulting from this usual method may be described as **normal secondary growth.** During normal secondary growth the usual devcopmlents that take place are :

(*i*) Formation of a complete ring of cambium by the formation of inter-fascicular cambial strips.

(*ii*) Secondary phloem is formed towards the outer side and secondary xxlem towards the inner side.

(*iii*) Only one ring of cambium is formed.

(*iv*) The position of the cambial ring is between primary xylem and primary phloem and the interfascicular cambial strips appear at the same level. The activity of cambium is uniform.

(*v*) Only one ring of cork cambium is formed in the extrastelar region.

There are many plants in which deviations from the normal type of secondary growth have been reported. They are very common in the flora of temperate regions and can be listed as under :—

(*i*) Unusual position of the cambium.
(*ii*) Abnormal functioning of the cambium.
(*iii*) Formation of more than one ring of cambia.
(*iv*) Formation of extra-stelar cambial ring.
(*v*) Formation of interxylary phloem.
(*vi*) Formation of interxylary cork.

The secondary tissue produced as a result of above mentioned deviations constitutes *abnormal or anomalous secondary growth.*

UNUSUAL POSITION OF THE CAMBIUM

Structural changes due to unusual position of the cambium are commonly found in the lianas or the woody climbers and can be listed as below :—

1. **Cambium raised into folds and ridges.** Schenck (1892) described this type of cambium in *Thinouia scandens* (Fig. 14.24). In this case the cambium is not in the form of a smooth or a circular ring but gives a folded appearance. It is thrown into ridges. This condition is

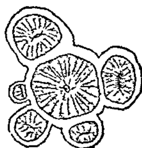


Fig. 14.24. T.S. through the stem of *Thinouia scandens* (Diagrammatic), showing anomalous secondary growth. (*After Schenck*)



Fig. 14.25. T.S. through stem (Diagrammatic) of *Serjania ichthyoctoma* showing anomalous secondary growth. (*After Schenck*)

seen in young stems. Later, the ridges of the cambium get separated and act each as individual cambium forming its own vascular cylinder or stele. As a result, the secondary structure of the stem consists of several steles each with its own secondary phloem and secondary xylem thus giving the mature stem a peculiar shape.



Fig. 14.26. T.S (Diagrammatic) through the stem of *Bauhinia longsdorffiana*, showing abnormal secondary growth (*After Schenck*)

2. Cambium in the form of separate strips. In some of the Sapindaceous tendril climbers *e.g.*, *Serjania ichthyoctona* (Fig. 14.25) and *Paullinia*, the primary stems possess separate strips of cambium which surround individual xylem strand or portions of primary xylem. As secondary growth proceeds, each strand becomes surrounded by its own cambium ring and thus separate cylinders of secondary vascular tissue are formed. Each cylinder has its own cambium with secondary phloem towards its outer side and secondary xylem towards its inner side. The stem in the secondary state appears to be made up of several stems that have fused together. Later, due to the development of periderm the outer layers of each vascular cylinder die and the stem in this condition is seen to be made up of several smaller stems that appear close to each other like the strands of a rope.

[illegible] condition similar to that described [illegible] ner. In this case the secondary [illegible] ıry phloem and xylem is in excess [illegible] ure of cambium ring into several strips and even the vascular cylinder is broken into numerous parts (Fig. 14.26).

ABNORMAL FUNCTIONING OF THE CAMBIUM

In many woody climbers or the lianas, the cambuim is normal in position but functions in an abnormal way. This produces peculiar types of secondary structures.

1. In *Aristolochia* (Fig. 14.27) and *Vitis vinifera*, the cambium ring is complete but the whole of the cambium does not produce secondary vascular tissue. Large portions of it produce parenchymatous cells that lead to the development of wood rays and the secondary vascular

tissue appears to consist of discrete vascular bundles. The same is the case in *Begonia fruticosa* (Fig. 14.28).

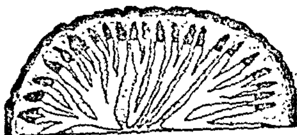


Fig. 14.27. T.S. (Diagrammatic) through stem of *Aristolochia* showing abnormal secondary growth.

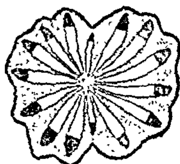


Fig. 14.28. T.S. (Diagrammatic) through stem of *Begonia fruticosa* (*After Schencka*)

2. In *Bauhinia rubiginosa* (Fig. 14.29), the secondary vascular cylinder appears in the form of ridges and grooves. This gives the stem a ridged appearance. This condition results due to the variations in the activity of the cambium ring. At certain places the cells of the cambial ring divide actively producing more secondary vascular tissues, whereas at other places it is inactive or the activity is very low. This leads to the formation of ridged secondary vascular cylinder. Flattened and strap-like stems in other species of *Bauhinia* (Fig. 14.30) are also due to restricted activity of the cambium in certain regions. In this case, the cambium is more active at the opposite sides. In some species of *Bignonia* a ridged and grooved secondary xylem cylinder is produced because the cambium, at certain places, produces more secondary xylem than at others. These ridges and grooves may appear simple (Fig. 14.13) or extremely complicated (Fig. 14.33).

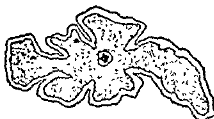


Fig. 14.29. T.S. (Diagrammatic) through stem of *Bauhinia rubiginosa*. (*After Schencka*)

3. In *Bignonia unguis-catae*, a transverse section of the stem, in



Fig. 14.30. T.S. through a flattened stem of *Bauhinia* sp. due to abnormal secondary growth. (*After Schencka*)

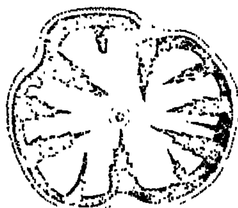


Fig 14.31 T.S. through the stem of *Bignonia* sp showing secondary phloem (dark) with step-like broadening. (*After Schenck*)

secondary state of growth, reveals four longitudinal furrows of secondary phloem wedged in-between the secondary xylem cylinder. These furrows are arranged in the form of a cross (Fig. 14.31). In each furrow of secondary phloem there are bars of sclerenchyma which permit it to maintain its shape and keep the secondary xylem on the side in position These four furrows develop as a result of the cambium producing more secondary phloem and less secondary xylem at four points.

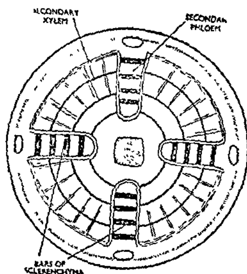


Fig. 14 32. Diagrammatic T.S. through *Bignonia unguis-catae* showing secondary phloem supported by bars of sclerenchyma wedged in-between secondary xylem.



Fig. 14.33. T.S. through *Bignonia* sp. showing complicated ridges and grooves. (*After Schenck*)

In one of the species the four longitudinal furrows of secondary phloem show step-like broadening of the secondary phloem (Fig. 14.31 shaded part). It is also due to variations in the activity of the cambium in the region of the furrows.

These longitudinal furrows of phloem wedged in-between the secondary xylem are of great use to the Bignoniaceous lianas and is an adaptation to their mechanical requirements. During strong winds the thick stems of these lianas bend and are prone to the pulling and cutting pressure, which will break the solid core of xylem. These furrows of secondary phloem act as shock absorbers.

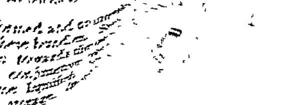
SUCCESSIVE RINGS OF CAMBIUM

In some gymnosperms like *Gnetum*, *Cycas*, and in some angiosperms e.g., *Securidaca lanecolata*, *Boerhaavia diffusa*, [illegible], the normal ring of cambium stops functioning after producing a secondary vascular cylinder of secondary phloem and secondary xylem. New cambium ring is formed outside i.e., centrifugally in the pericycle or in the secondary parenchymatous tissue formed by the first cambial ring and then in the cortex. Like this, successive cambial rings appear and produce alternating concentric rings of secondary vascular tissue consisting of secondary phloem and xylem. In *Gnetum* (Fig. 14.34), the cambial rings formed, after the death of the normal cambium, produce discrete secondary vascular bundles. Metcalfe and Chalk (1957) reported the formation of successive cambia in 28 dicot families. The common ones are: *Amaranthaceae, Chenopodiaceae, Menispermaceae, Nyctaginaceae, Rubiaceae, Bignoniaceae, Cruciferae, Convolvulaceae, Compositae, Papilionaceae etc.*



Secondary Growth in Boerhaavia diffusa (Figs. 14.35 and 14.36). It is an example of an angiosperm (Nyctaginaceae) in which successive rings of cambia are produced. It was studied in detail by Maheshwari (1930). The fascicular cambial regions (present between primary phloem and xylem of the outer ring of bundles) subsequently become connected by interfascicular cambium (Fig. 14.35, 14.36) thus producing a cylindrical meristem which gives rise internally to secondary xylem in regions where new bundles are formed and conjunctive parenchymatous ground tissue [illegible] formed opposite to secondary xylem towards the [illegible] fascicular ground tissue is called conjunctive [illegible] elongated living cells which become lignified [illegible] substitute fibres and vessels [illegible]

Fig. 14.34. T.S. [illegible] showing [illegible] and discrete [illegible] bundles.



the cambium also gives rise to thin-walled cells, called storage parenchyma towards outside. After a time this cambium ceases to function, and a new meristem arises, under favourable conditions, from the parenchymatous cells cut off by the first cambium towards the outer side and from the pericycle cells lying external to the phloem groups. These cells divide and become distinguished as strips of cambium. These cambial strips of the second cambial ring are extra fasicular regions external to the phloem. Elsewhere the secondary cambial ring is derived from the outer parenchymatous cells formed by the first cambial ring and is interfascicular The extra fascicular and inter-

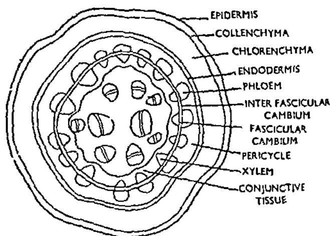
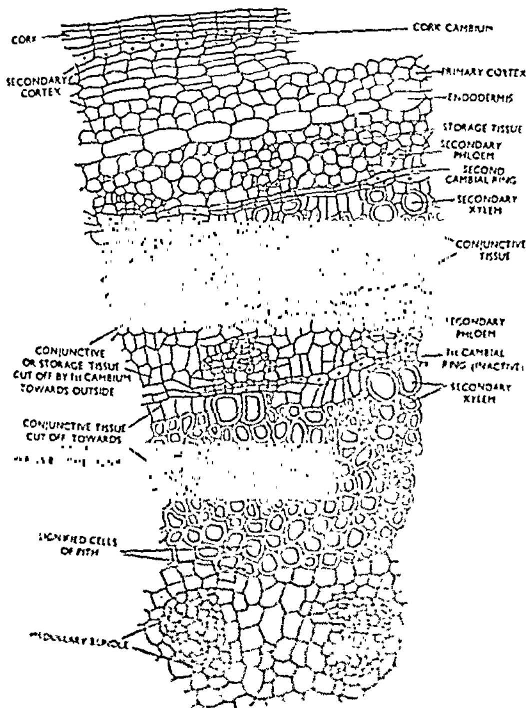


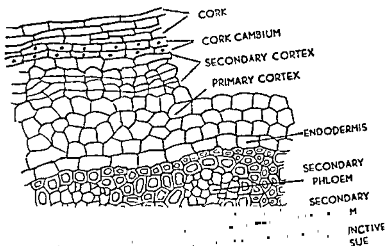
Fig. 14 35 T S (diagrammatic) Stem of *Boerhaavia diffusa* showing complete ring of cambium and formation of conjunctive tissue.

fascicular strips may unite to form a complete cambial ring. These cells divide tangentially. It functions in a way similar to the *first ring* of cambium. It also becomes inactive and a third ring asises outside it. Like this four or five cambial rings are produced and give rise to successive rings of collateral bundles embedded in the canjunctive tissue. *The secondary vascular bundles were previously believed to* originate in the parenchymatous portion of the *pericycle but* Maheshwari (1930, 42-61) proved it to be wrong in case of *Mirabilis jalapa* and *Boerhaavia*. In these cases these bundles, as *described* above, arise from the cambial ring. In prostrate stems, *there is more* growth on the lower side than on the upper.

Cork cambium is formed in the hypodermal collenchyma and produces cork towards the outside and secondary cortex towards *the inner* side. The secondary phloem consists of sieve tubes, *companion cells* and phloem parenchyma.

Secondary Growth in Bougainvillea. (Fig. 14.37). *It is similar to Boerhaavia* because in this case also more than one cambial rings are formed. The second cambial ring arises external to the first *after the* first one has become inactive. Here also the secondary vascular tissues


CORK
CORK CAMBIUM
SECONDARY CORTEX
PRIMARY CORTEX
ENDODERMIS
STORAGE TISSUE
SECONDARY PHLOEM
SECOND CAMBIAL RING
SECONDARY XYLEM
CONJUNCTIVE TISSUE
SECONDARY PHLOEM
1st CAMBIAL RING (INACTIVE)
CONJUNCTIVE OR STORAGE TISSUE CUT OFF BY 1st CAMBIUM TOWARDS OUTSIDE
SECONDARY XYLEM
CONJUNCTIVE TISSUE CUT OFF TOWARDS
LIGNIFIED CELLS OF PITH
MEDULLARY BUNDLE



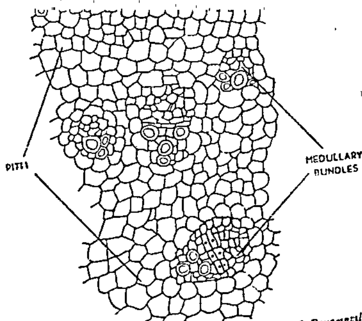
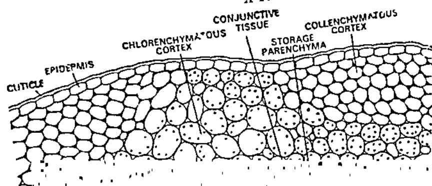


Fig. 14.37. T.S. (portion in detail) of stem of *Bougainvillea* showing secondary growth. Note the thick-walled conjunctive tissue. Cork cambium has also appeared and cork layers formed.

are produced only by the fascicular strips of the first cambial ring. The successive rings also produce secondary vascular tissues at certain

places and not all over. This leads to the formation of separate or discrete secondary vascular bundles. It differs from *Boerhaavia* in that the conjunctive tissue in which the secondary bundles are embedded is sclerenchymatous (Fig. 14.37) with the result that the xylem of the embedded bundles cannot be demarcated from the conjunctive tissue. The secondary phloem of these bundles can be seen in the form of islands of thin-walled cells (sieve-tubes, companion cells and phloem parenchyma). This should not be regarded as inter-xylary phloem.

Recently, Stevenson and Popham (1973) studied the development of an *extrastelar cambium* or the *primary thickening meristem* in *Bougainvilea spectabilis* in the young seedlings Their observations are quite contrary to those of Maheshwari (1930). They have concluded from their study that a primary thickening meristem originates in the pericycle. It first appears in the base of the primary root after 6 days of germir [illegible] roof grows. In seedlin [illegible] the base of the hypocc [illegible] After 60 days of germination this meristem starts appearing at the base of the first internode. Later, it develops into a complete cylinder in the axis of the young seedling. There is no interfascicular cambium formed in the stem. So entire secondary growth is affected by the complete cylinder of primary thickening meristem differentiated in the pericycles external to the outer ring of vascular bundles. As a result of its activity conjunctive tissue is cut off internally as well as externally. New secondary vascular bundles or *desmogen strands* originate in two different ways :—



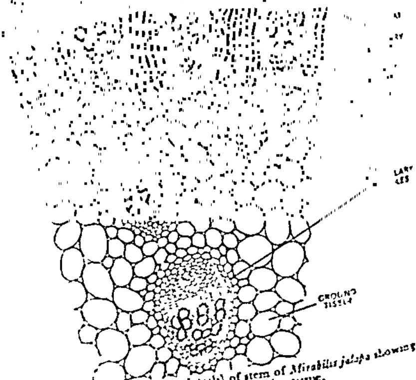


Fig. 14.33. T.S. (portion in details) of stem of *Mirabilis jalapa* showing secondary growth and thick-walled conjunctive tissue.

The secondary xylem of the desmogen strands has both tracheids and vessels. Desmogen strands appear acropetally in conjunctive tissue.

Esau and Cheadle (1969) have also observed these sequences of events in the secondary growth of the stem of *Bougainvillea spectabilis.*

Pfeiffer (1926), Metcalfe and Chalk (1950) and Fahn (1967) as a result of erroneous observations regarded the phloem of desmogen strands as included phloem (intraxylary phloem). This is not correct because phloem in desmogen strands is not surrounded by xylem on all sides. Xylem occurs only interior to the phloem These desmogen strands are surrounded by lignified conjunctive tissue developed as a result of elongation and lignification of parenchymatous conjunctive tissue cells.

Balfour (1965) stated that primary thickening meristem in *B. spectabilis* originates in cortical parenchyma of the stem Her observations were not supported by those of Stevenson and Popham (1973).

Secondary Growth in Mirabilis jalapa (Fig. 14 38)

It is exactly similar to *Boerhaavia diffusa* and can be summarised as below :

1. Distinct strips of interfascicular cambium arise in the medullary rays between the outer ring of normal bundles. It joins with the fascicular cambial strips to form a complete ring of cambium (Maheshwari, 1930, pp. 55, 56). It is incorrect as stated by earlier workers (De Barry, 1884) that an entirely new cambium arises *de novo* in the pericycle outside the ring of bundles (extrastelar).

2. The secondary tissues produced by this cambium cylinder consists of secondary xylem and phloem in the intrafascicular region ; the interfascicular strips produce only conjunctive tissue and storage parenchyma.

3. The conjunctive tissue produced internally by interfasciular cambial regions consists of thin-walled, elongated cells, which may later become lignified.

4. The first formed or the original cambium becomes inactive after a time, another cambium arises outside it by tangenial division of the parenchyma cells cut off towards outside by the original cambial layer. This new cambial ring is formed outside the primary phloem and runs through the cells of the pericycle.

5. The second cambium also ceases to function, and a third cambium ring arises outside by the tangential divisions of the parenchyma cells cut off by the second ring externally.

6. The process of secondary vascular tissues formed by these cambial rings is similar in all respects. Secondary phloem and xylem are always formed oppposite to each other so as to give rise to secondary bundles that are collateral.

Mikesell and Popham (1973) studied the development of primary thickening meristem in the young seedlings of *Mirabilis jalapa.* They observed this meristem at the base of the stem (base of first internode) in 12 day old seedlings. The primary thickening meristem appears in the inner cortex or the pericycle and completely surrounds the ring of primary vascular bundles. The meristem produces conjunctive tissue towards inner side. In this tissue, groups of meristematic cells differentiate. These are called *prodesmogen strands*. In these strands, secondary phloem, secondary xylem and desmogic cambium differentiate to form secondary vascular bundles or the *desmogen strands*. These obserations are quite contrary to those of Maheshwari (1930). The conjunctive tissue may later become lignified.

Hamner (1938) concluded that the primary thickening meristem is composed of cambial segments that originate in the pericycle opposite primary vascular bundles of outer ring and become continuous with the inter-fascicular cambial strips in the medullary rays between the vascular bundles of the outer rings. Mikesell and Popham (1973) did not observe any interfascicular cambial strips and according to them no such strips are even observable in Hamn er's photographs.

The above observations confirm De Barry's (1884) observations on *Mirabilis jalapa.*

EXTRASTELAR CAMBIUM

In some dicot families *e.g., Amaranthaceae, Chenopodiaceae* etc., the first ring of cambium arises *de novo* in the pericycle. Such a ring of cambium, in contradistinction to the normal type, which develops between the vascular bundles, is called *extrastelar cambial ring* (Figs. 14.10 and 14.38). In such cases no normal type of cambial ring is formed. The activity of the extrastelar cambium differs in different plants.

In *Amaranthaceae* and *Chenopodiaceae*, the extrastelar cambium arises in the pericycle either in the form of a complete ring (*Amaranthus*) or in the form of separate strips or arcs of meristem (*Achyranthes*). In the former case the secondary vascular elements are arranged in concentric circles and are collateral. In the latter case, the vascular bundles are collateral and irregularly scattered. In *Celosia cristata, Amaranthus blitum*, *A. viridis* and *Bosea yervamora*, the conjunctive tissue between the bundles is parenchymatous. In *Aerva scandens*, the conjunctive tissue is lignified and sclerencymatous. The successive rings of vascular bundles produced by different cambial rings are separated by concentric zones of ground tissue. The ground tissue of these zones may be (*i*) parenchymatous, (*ii*) sclerenchymatous, and (*iii*) in some cases some zones are parenchymatous and others sclerenchymatous. Schinz (1934) considers the parenchymatous secondary ground tissue as comparable to pith. In this condition the vascular bundles embedded in this ground tissue appear as medullary bundles that are secondary in origin and should not be regarded as such *e.g., Celosia cristata.* In some species *e.g., Achyranthes aspera, A. coyeni* and *Amaranthus viridis*, the medullary bundles are primary in nature and are the

true medullary strands. In *Froelichia gracilis*, *Arthracrua* and *Gomphrena globosa*, there are no medullary bundles. In these species the secondary growth gives rise only to a peripheral ring of secondary vascular tissue and no bundles are present within this ring.

Joshi (1973, pp. 3—9) considers [illegible] of cambium as a primitive feature anc [illegible] evolution the anomalous secondary [illegible] secondary cambia became reduced to [illegible] tion combined with the conversion of secondary parenchyma into sclerenchymatous conjunctive tissue leads to the development of interxylary phloem of the *forminate type*. The author does not conform to this view as the included phloem is surrounded by xylem on all sides and not by conjunctive parenchyma, whose cells become lignified.

Secondary Growth in Chenopodium (Fig. 14.39)

In *Chenopodium*, secondary growth begins by the formation of extrastelar cambium in the pericycle. This first ring of extrastelar cambium is continuous and after producing a layer of thin-walled ground tissue produces secondary vascular bundles. Some cells of the secondary conjunctive tissue become meristematic and form groups of *predesmogen strands*. In these strands secondary phloem distinguishes first and later secondary xylem towards inner side of phloem, thus forming a secondary vascular bundle or a *desmogen strand*. The formation of thin-walled ground tissue in the beginning pushes the primary bundles towards the centre and they appear as medullary bundles. These primary bundles may grow in thickness by the activity of their fascicular cambia and contain secondary tissues. Later, the first extrastelar cambial ring produces a number of secondary vascular bundles and thick-walled conjunctive tissue.

Successive rings or arcs of cambium produced in the pericycle lead to the formation of regular or irregular rings of secondary vascular bundles. Arcs of cambia develop external to the phloem thus burying it in the conjunctive tissue. The ground tissue (in which the bundles are embedded) and the interfascicular conjunctive tissue are sclerenchymatous and sometimes it becomes difficult to distinguish the secondary-xylem from them. The thin-walled phloem groups are quite prominent and appear as interxylary phloem, but actually they are not interxylary as these are not surrounded by xylem.

Secondary Growth in Amaranthus (Fig. 14.12). In *Amaranthus*, the primary vasculature consists of a normal ring of vascular bundles and a large number of primary medullary bundles Secondary growth begins by the formation of extrastelar cambium in the pericycle. It cuts off secondary vascular bundles and interfascicular conjunctive tissue, which, unlike *Chenopodium*, is parenchymatous (Fig. 14.12). The cambium cuts of cells only towards the inner side. At certain places these cells develop into secondary vascular bundles and at other places these cells give rise to interfascicular and parenchymatous conjunctive tissue.

Secondary Growth in Achyranthes aspera.

In *Achyranthes aspera*, the extrastelar cambium appears in the form

of small arcs of meristematic cells in the pericycle. These meristematic arcs or cambial strips produce secondary vascular bundles that are irregularly distributed in the ground tissue. The conjunctive tissue produced by the cambium is lignified in this case and sometimes it is difficult to distinguish between the secondary xylem groups of the various bundles and the thick-walled cells of the conjunctive tissue. The phloem, however, appears in the form of distinct patches and gives

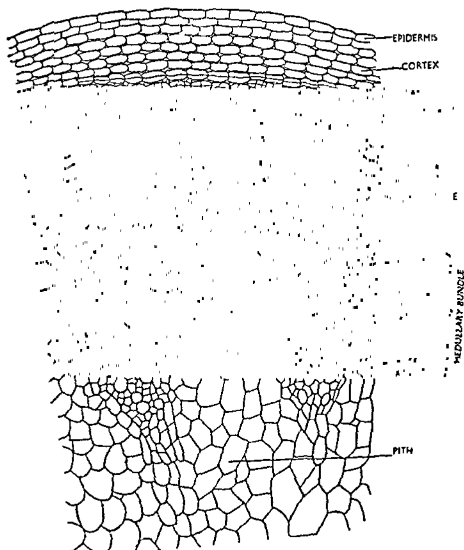


Fig 14.39 *Chenopodium album*. T.S. portion of stem (detail) showing extrastelar cambium in pericycle and medullary bundles. The medullary bundles also show secondary tissues. (*After Eames and Macdaniels*).

the appearance of included or inter-xylary phloem. Such an included phloem is usually referred to as *'forminate'* type.

The definition of an included phloem is "the phloem that develops within secondary xylem". In these anomalous cases the phloem being

thin-walled and the surrounding conjunctive tissue being thick-walled, it (phloem) appears to be included. Actually, *it is* not, because it is surrounded only by lignified cells that are neither tracheids nor vessels. The author does not agree with the observation that it is of forminate type. It is not a case of included phloem.

In some species of *Achyranthes*, the conjunctive tissue is parenchymatous.

INTERXYLARY PHLOEM

It is also called *included phloem* and develops within the secondary xylem. It has been reported in 25 families of the dicotyledons. It develops variously in various plants. Three usual types have been reported. In a number of species of Amaranthaceae (*Achyranthes* sp. *Alternanthera* some species of *Amaranthus*, *Bosea*, *Celosia*, *Pupalia*, etc.) and Loganiaceae (*Strykhnos*), the included phloem develops in the following manner :—

Small arcs or strips of cambium develop. These strips divide and form cells which differentiate into secondary phloem and secondary xylem. Now these strips become functionless. Now strips of cambium develop external to the secondary phloem groups. The margins of these new cambial strips join with those of the old inactive ones. These new cambial strips (present outside the secondary phloem) start functioning normally and produce xylem on the outside of the phloem, thus, making it included. This phloem group has now xylem on its either side and becomes included within the xylem. This type of cambial activity continues at several places in the stem and results in the formation of secondary xylem with scattered groups of *interxylary phloem*. This type of included phloem was termed as '*concentric type*' by Pfeiffer (1926). It has also been described by Iljin (1950).

In *Leptadenia*, *Combretum*, *Salvadora persica* (Singh, 1944) and in *Thunbergia mysorensis* (Mullender, 1947), included phloem arises as a result of small portions of cambium producing secondary phloem towards the inside instead of secondary xylem. Later, these very segments start functioning normally and produce secondary xylem towards inside. This way the secondary phloem formed earlier becomes embedded in the secondary xylem and is known as *included phloem* or *interxylary phloem*.

In some Chenopodiaceous stems *e.g.*, *Beta* (Artsehwager, 1926), the *included phloem* arises in the following manner :—

In this case the successive cambial rings have a developmental relationship. This cambial ring cuts off cells towards the inner side as well as outer side. The inner cells after a number of divisions differentiate into secondary phloem and secondary xylem. The outer cells differentiate into the next outer cambium which replaces the previous one. This new cambium functions in the same manner. The phloem produced by the previous cambium is overlaid by the xylem produced by the new cambial ring, thus making it included phloem. This process

continues and several patches of included phloem can be recognised in a transverse section.

The detailed structure of *Leptadaenia* (Asclepiadaceae) has been described earlier in this chapter (see Fig. 14.21).

Included phloem is of great significance to some xerophytic plants which possess it. In such plants the included phloem remains active or functional even during long summer drought. It retains its functional capacity even when other tissues dry and become nonfunctional. These strands of functional included phloem serve to carry food to the buds which develop into branches at the commencement of favourable season.

INTERXYLARY CORK

A cork layer that develops between the two growth rings of secondary xylem is called interxylary cork. It has been recorded in *Artemesia tridentata* (Compositae; Record and Hess, 1943), *Epilobium angustifolium* (Onagraceae ; Moss, 1936). In these species, the interxylary periderm is produced by a cork cambium, which develops in parenchmatous zone in secondary xylem. Presence of such a cork in perennating organs is considered to enable them to overcome conditions of drought or drouth.

15

THE LEAF

The leaves usually possess a more or less expanded portion, the **blade**, which may or may not be borne on a stalk, the petiole. The blade is composed of veins and of the green parts between the veins, the **mesophyll** ; the latter is the seat of food manufacture or photosynthesis and the former are organs of support and transportation. In many cases, the leaves are scale-like and take no part in food-making. In some cases, these scale leaves serve to store food material. They also protect the younger parts. These scale leaves are called **cataphylls.** The cotyledons are the first green leaves that are produced by the plant.

ANATOMY OF ANGIOSPERM LEAF

The leaf consists of three usual tissue systems—the dermal tissue system, the ground tissue system, and the vascular tissue system.

[illegible] y do [illegible] is an [illegible] e layer of cells that are closely packed. The upper epidermis possesses cells that appear irregular when seen in surface view and more or less rectangular in cross-section. Often, the individual epidermal cells look like pieces of a jigsaw puzzle. The outer walls of the epidermal cells are cutinized. The thickness of the cuticle varies with species. It may form a thin layer in ordinary herbaceous plants, like sunflower, alfalfa cucurbita etc., or it may be very thick as in most of the xerophytic plants, like *Hakea* (Fig. 15.8.) and *Dianthus co yophyllus* (Fig. 8.5 B). In *Salix glaucophylla* the cuticle layer is again covered by a thick layer of wax grains constituting a glaucous bloom. In some plants like *Ficus elastica*, the upper epidermis is three-layered and its walls are highly cutinised (Fig. 8.5, A). In a succulent species of *Begonia*, the upper epidermis is three-layered and the lower epidermis is two-layered (Fig. 8.9). Certain epidermal cells of many plants bear hair. Some hair are merely unicellular, elongated epidermal cells. In others the hair are filamentous and made up of two or more cells (Figs. 8.10 and 8.11) resulting from the growth and division of epidermal cells. The epidermal cells in some cases *e.g.*, *Atriplex portulacoides*, are thick-walled.

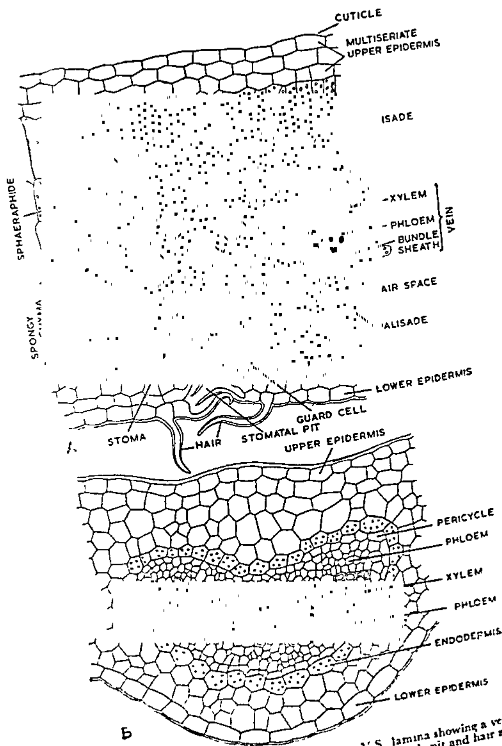


Fig. 15.1. (A—B). Leaf of *Nerium oderum*. A, V.S lamina showing a vein, multiseriate epidermis, well developed palisade, stomatal pit and hair and stomata. B, section passing through the mid-rib.

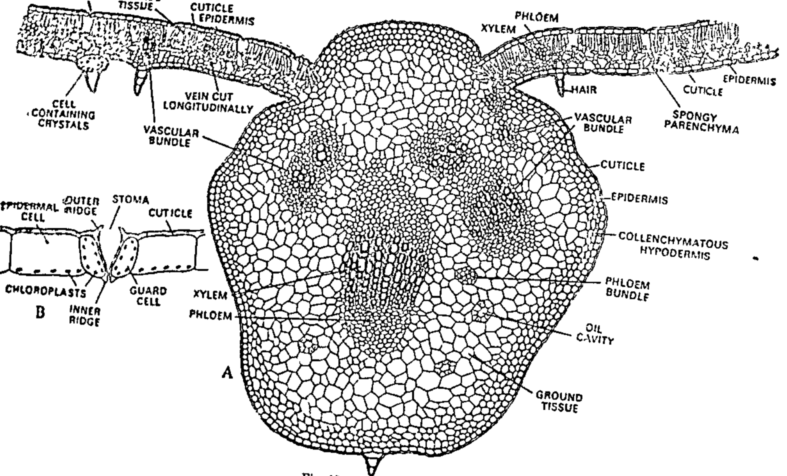


Fig. 15.2. T.S. leaf of *Helianthus*

Groups of collenchymatous cells are present next to the lower epidermis in *Nymphaea* (Fig. 15.7).

Branched hair are not uncommon. Glandular hair are also present on the upper and lower epidermises of many plants. As the leaf lamina matures, the hair often shrivel up and disappear, but they may presist. The strong odours given off by mints are due to volatile oils secreted by the terminal cells of glandular hair on the leaves. In *Atriplex* both the upper and the lower epidermal layers are covered with numerous vesiculate salt-secreting trichomes.

Both the upper and the lower epidermises contain stomata. They are, however, abundant on the lower epidermis. In the floating leaves of *Trapa bispinosa* (Fig. 15.4) and some other floating hydrophytes (Fig. 15.5), the stomata are present only in the upper epidermis. The stomata may be in level with other epidermal cells as in most of the mesophytes, or raised above the epidermal cells as in hydrophytes, or they may be sunken in definite pits as in xerophytes *e.g.*, *Nerium odorum* (Fig. 15.1). The guard cells of the stomata possess chloroplasts and are thus clearly demarcated from the rest of the epidermal cells.

In *Opuntia basilaris,* all the cells in the epidermis possess chloroplasts (Freeman, 1973).

Mesophyll. The mesophyll tissue lies between the upper and the lower epidermises. Its cells are characterised by the presence of abundant chloroplasts and lots of intercellular spaces. In some leaves (hydrophytes), it is homogenous and in others (xerophytes and majority of mesophytes) it is made up of two types of cells. The cells lying below the upper epidermis are elongated and arranged in a compact palisade-like layer. The layer is called palisade parenchyma (Fig. 15.1). Below the palisade parenchyma the cells are loosely arranged and have varying shapes. This region is called spongy parenchyma (*Fig. 15.1*). *The extent of* palisade varies in various types of leaves. It may consist of (Fig. 15.3) a single layer (*e.g.*, *Rose, Lawsonia*), below the upper epidermis or there may be more layers than one (*Nerium*). In *Atriplex portulacoides,* the palisade tissue develops in abundance next to both the epidermal layers and spongy parencyma is reduced only to small strip in central portion of the leaf. In extreme cases *e.g.*, *Greggia camporum*, *Lactuca scarida* and *Sphaeralcea incana*, the entire mesophyll is differentiated as palisade tissue. In *Atriplex halimus*, both the epidermal layers are followed by a single layer of large and colourless cells that store water [illegible] some of the cells in these layers [illegible] s is the many- [illegible] asts. In *Atriplex canescens* and *Eucalyptus* a single layer of palisade is found on either side of the leaf. Such leaves are called **isobilateral** or **isolateral** or **equifacial**. In *Portulaca oleracea*, there is a festoon of funnel-shaped cells around the veins. These cells contain chloroplasts at their bases. Such cells are again surrounded by elongated palisade-like cells that are curved towards the bundle and have scattered chloroplasts. In the

albescent leaves of *Abutilon* (Fig, 15.6) palisade cells are found only in one half of the blade and are absent in the other. The lower epidermis contains chloroplasts. The cells of spongy parenchyma in one half [illegible] lack chloroplasts. In [illegible] the total amount of [illegible] parenchyma cells.

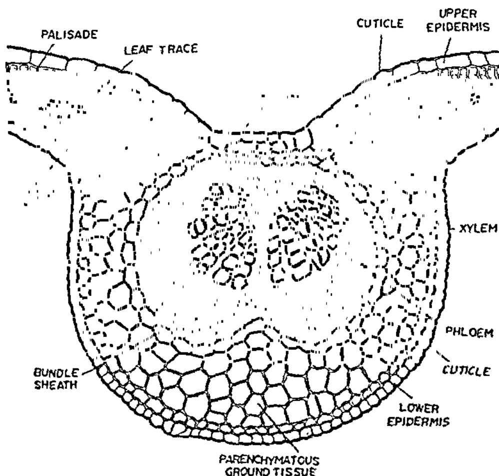


Fig. 15.3. T.S. Leaf of *Rosa* sp.

In Hakea, elongated stone cells (Fig. 15.8) or osterosclereids are present among the palisade cells. They give strength to the leaf.

Next to the palisade tissue, just beneath it, commonly making up *the greater part of the thickness of the leaf, is a region of rounded or* irregularly-lobed cells which are loosely packed since each of the cells has but a small portion of its surface in contact with the surface of [illegible] **spongy tissue.** [illegible] r spaces. In float- [illegible] *and Nymphaea*

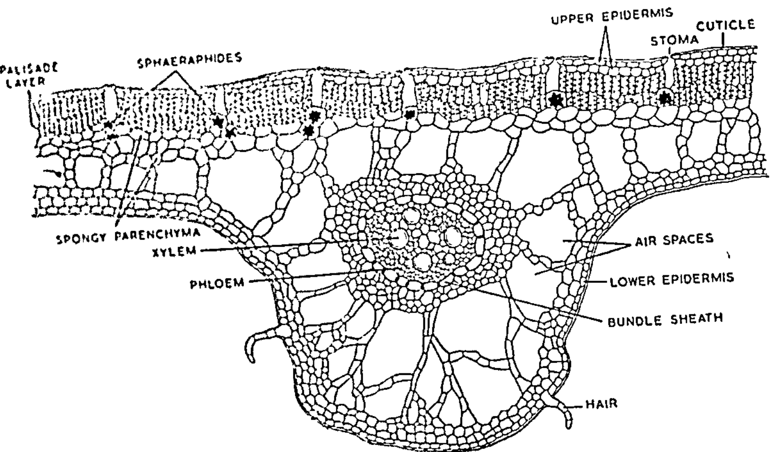


Fig. 15.4. T.S. floating leaf of *Trapa bispinosa*, showing detailed internal structure. Note that the stomata are restricted to the upper epidermis alone.

the spongy parenchyma is traversed by large air-spaces (Fig. 15.4). In *Nymphaea*, the air spaces are present even around the mid-rib (Fig.15.7) and possess branched sclereids in their partition walls. The cells in this region also contain chloroplasts but the proportion of the chloroplasts is much less as compared to the cells in the palisade-region. Next to the spongy parenchyma is the **lower epidermis**, whose cells have a structure similar to that of the upper epidermis. The lower epidermis is characterised by the presence of a large number of stomata. Each stoma

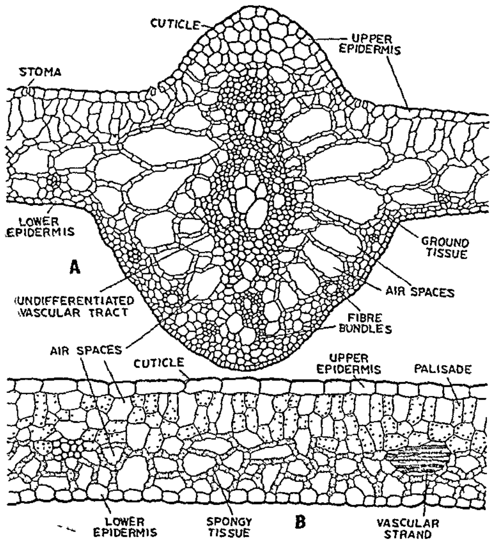


Fig. 15.5. (A, B). T.S. Leaf of *Sagittaria.*

A. Section passing through mid-rib and portion of lamina on either side. Note the extensive air-spaces.

B. Section passing through a portion of the lamina. The stomata are . to the upper epidermis.

opens into an intercellular space called the **substomatal cavity,** which, in turn, is continuous with the spaces between the cells of spongy tissue.

Fig. 15.6. T.S. Albescent leaf of *Abutilon*; to the right of the ... two rows of palisade ... without palisade cells. ... The spongy tissue ... reas towards left side it is colourless.

In *Trapa bispinosa* a cell or cells at the floor of the substomatal cavity contain star-shaped crystals of calcium oxalate, called the **sphaeraphides** (Fig. 15.4). The intercellular spaces in the spongy tissue are, in turn, connected with each other and with such spaces that may occur between the palisade cells. Hence, the stomatal and the intercellular spaces in the mesophyll tissue of the leaf constitute an aerating system lined with a large area of wet wall surface, which permits free gaseous exchange between the atmosphere and the interior of the leaf. In most of the leaves the stomata are restricted to the lower epidermis. Such leaves are called **hypostomatic** *e.g.*, *Nerium*. In **amphistomatic** leaves, the stomata are found on both the surfaces of the leaf.

Vascular System. The venation of the leaf which consists of a midrib ... syst ... end ... dissolved in water to the mesophyll cells and take away the manufactured food synthesized in the mesophyll cells. The veins of a leaf are vascular bundles which are continuous through the petiole with the vasculature of the stem. The mid-vein or the mid-rib of a leaf shows a wide range of variations in the arrangement, amount and extent of the vascular tissue. In many dicot leaves, like *Sanguisorba*, *Cannabis*, *Nerium*,

Prunus etc., there is only a single vascular bundle in the mid-rib. In *sunflower, Vitis*, etc., the number of vascular bundles is many. In *Nymphaea*

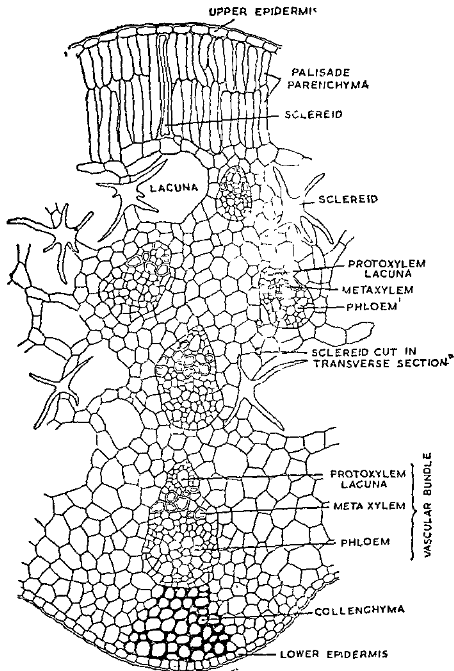


Fig. 15.7. T.S. leaf of *Nymphaea* passing through the mid-rib. Note the arrangement of the vascular bundles, the sclereids, collenchyma above the lower epidermis and the lacunae or the air-spaces.

(Fig. 15.7) there are many distinct vascular bundles in the mid-rib. They lie scattered. There is no bundle-sheath or endodermis. Sometimes, a distinct bundle sheat and a pericycle layer are also present. In *Hakea*, the vascular bundles are capped with sclerenchymatous patches

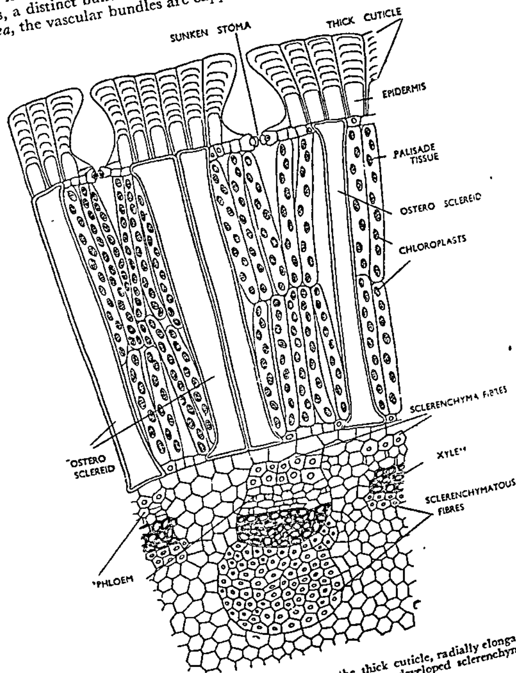


Fig. 15.8. T.S. **Leaf of** *Hakea*. Note the thick cuticle, radially elongated epidermal cells, osteosclereids, and extensively developed sclerenchymatous cap over vascular bundles of the vein.

on either end (Fig. 15.8). The sclerenchyma is well-developed towards the ventral side. These patches are called *bundle caps.* The spongy parenchyma cells around the mid-rib are compactly arranged. In *Nymphaea*, the cells around the mid-rib are loosely arranged and there are distinct air-spaces (Fig. 15.7)that contain sclereids in their partition walls. The palisade tissue is also absent in this region and its place is taken by ordinary parenchyma cells, that are generally devoid of chloroplasts. These cells in some species are collenchymatous. The vascular bundles in a mid-rib are conjoint and collateral. The phloem is present towards the lower side and xylem facing the upper side. In stems, the vascular bundle has xylem towards the inner side and phloem towards the outer side. Thus, in an outward extension of such a bundle into a leaf, the xylem lies towards the upper side of the blade and phloem towards the lower side. In *Juglans*, the vascular bundle is surrounded by a sclerenchymatous sheath and the phloem completely surrounds the xylem. The xylem and the phloem in a vascular bundle are made up of similar kinds of cells as found in the stem. The xylem consists of vessels, tracheids parenchyma, and even fibres. The phloem is made up of sieve-tubes, companion cells, and phloem parenchyma. Cambial strip has been recognised in the vascular bundle of mid-rib in *Nerium*. In the smaller veins, the vessels may be absent and their place is taken up by the tracheids. As the branch veins arising from the mid-rib and the main vein become progressively smaller, the phloem and xylem contain fewer elements. Each of the ultimate fine veins in which the vascular system terminates may lack phloem and may be but a



Fig. 15.9. *Impatiens parviflora* showing bundle sheath extending right up to the termination of the vascular bundle. (*After Schench*).

single tracheid in diameter. In the leaf of *Syringa*, the phloem is present along with the xylem upto its termination in the mesophyll. The vascular bundles are always surrounded by a sheath. It is generally parenchymatous and may be single-layerd or doubled-layered. The sheath may extend uninterruptedly even upto the finest ramifications of the vascular strands *e.g.*, *Impatiens parviflora* (Fig. 15.9).

In *Fagus sylvatica* (Fig. 15.10) the bundle sheath is sclerenchymatous. Bailey and Nast (1944) have reported the occurrence of sclerenchymatous bundle-sheath in most of the members of the family Winteraceae. In *Amaranthus edulis* and *Atriplex lentiformis*, the bundle-

sheath is one-layered and parenchymatous. Its cells contain abundant chloroplasts that store large amounts of starch. The bundle-sheath is surrounded by a layer of palisade cells. The presence of abundant starch in the chloroplasts of bundle-sheath cells of these dicots is a character that brings them closer to some monocots, like sugar-cane and corn (see W.M. Laefsch, 1968).

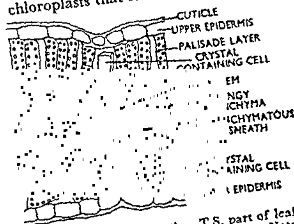


Fig 15 10. *Fagus sylvatica.* T.S. part of leaf showing detailed internal structure. Note the vascular bundle is present between the crystal-containsng cells and is enclosed within a sclerenchymatous sheath.

In *Fagus sylvatica,* the vascular buddle lies between two crystal-containing cells (Fig. 15.10).

In *Atriplex halimus,* the sheath surrounding the vascular bundles is incomplete towards the lower epidermis. The cells are rich in chloroplasts as compared to the surrounding mesophyll cells.

DESCRIPTIONS OF SOME COMMON DICOTYLEDONOUS LEAVES

Leaf of Boerhaavia. The leaves in *Boerhaavia* are dorsiventral and exhibit xerophytic characters.

In *B. diffusa* (Fig. 15.11), there is a thick cuticle on both the epidermal surfaces. The epidermal cells are of unequal sizes. The stomata are

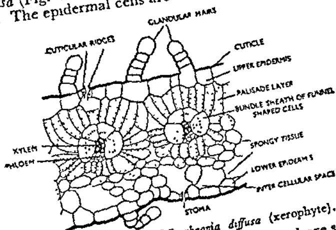


Fig. 15.11. T.S. leaf of *Boerhaavia diffusa* (xerophyte).

present on both the upper and the lower surfaces and are slightly sunken. They have cuticular ridges both above and below (Fig. 15.11). The palisade cells are bent in such a way that they tend to converge around the bundles. The veins are surrounded incompletely by a

festoon of funnel-shaped cells that constitute the bundle sheath. These cells have chloroplasts aggregated near their bases. The chloroplasts in the palisade are irregularly scattered. The bundle-sheath is absent opposite the phloem group. Bundle sheath is absent around the vascular bundle of the mid-rib. Dastur and Saxton (1922) reported the presence of tanin in the cells of bundle sheath surrounding the vascular bundle of the veins. The xylem is not well-developed. Both the epidermal surfaces are covered with glandular hair. There is a distinct ventral groove present opposite the mid-rib. Bundles of needle-like crystals or raphides are present in the spongy parenchyma cells.

In *B. repanda*, the stomata are present only on the ventral surface. The stomata have a cuticular ridge only on the upper side. The epidermal cells are of markedly unequal sizes and different shapes (Fig. 15.12). The lower epidermis has collenchymatous cells in the mid-rib region. The mesophyll has palisade cells below the upper epidermis and spongy tissue towards the lower epidermis. No peculiar orientation of

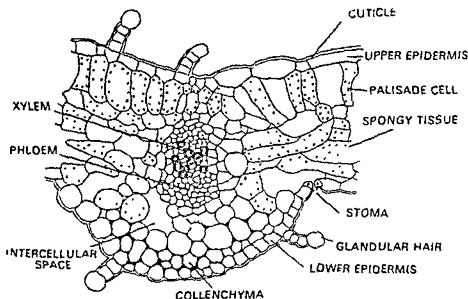


Fig. 15.12. V.S. leaf of *Boerhaavia repanda* passing through mid-rib.

palisade cells around the veins is noticeable in this species. There is no ventral groove opposite the mid-rib. In other respects it, resembles in its anatomy the leaf of *B. diffusa*.

Leaf of Victoria regia. A cross-section through a portion of this leaf (Fig. 15.14) shows the following structures :—

Epidermis. Both the upper and the lower epidermises are composed of single layers of thin-walled cells. The stomata are confined only to the upper epidermis. They are evenly distributed and are raised above the surface of the epidermis.

Mesophyll.
The palisade is
a single row of

have intercellular spaces between them. The spongy parenchyma is occupied by large air-spaces separated by partitions composed of parenchymatous cells arranged in a single row.

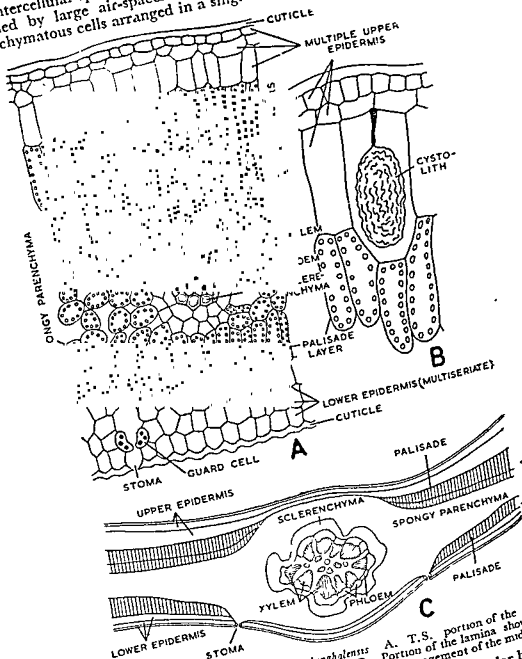


Fig. 15 13. (A—C). Leaf of *Ficus benghalensis* A. T.S. portion of the leaf passing through lamina, showing a vein B. Portion of the lamina showing cystolith. C. Outline figure of the leaf showing the arrangement of the mid-rib.

The vascular system consists of a number of small vascular bundles. The bundles have undifferentiated vascular elements.

Thin cuticle, presence of large air-spaces, loosely arranged palisade cells, raised stomata and poorly developed vascular sysem are the hydrophytic characteristics.

Leaf of Nymphaea advena. The leaf is dorsiventral and a transverse section (Fig. 15.7) reveals the following structures :—

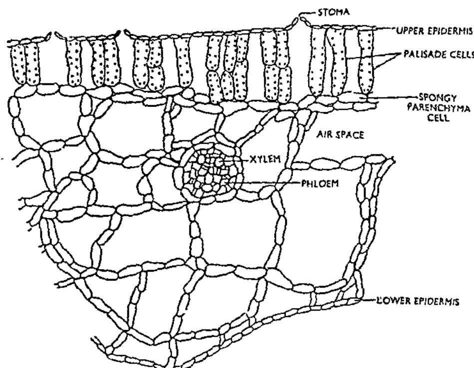


Fig. 15.14. A V.S. leaf of *Victoria regia*, showing abundant aerenchyma, loosely arranged palisade, stomata in the upper surface, and a single vascular bundle.

Epidermis. There are two layers of epidermis (upper and lower) and are composed of single layers of thin-walled cells. The cells in the upper epidermis are small. The stomata are confined only to the upper epidermis. The cuticle is thin and almost absent on the lower epidermis. The lower epidermis contains slime glands also

Mesophyll. Th[illegible] parenchyma. Th[illegible] [illegible] strands. A characteris- t[illegible] which project into the a[illegible] he lacunae and have [illegible] places of contact with the cells of the partitions.

Vascular system

The vascular system consists of a number of vascular bundles in the mid-rib region. A large vascular bundle is distinguishable towards the lower epidermis. It consists of phloem towards the lower epidermis

and xylem towards the upper epidermis. One or two bundles towards the upper epidermis have phloem towards the upper epidermis and xylem towards the lower epidermis. Xylem lacks vessels and is poorly developed.

The hydrophytic features of this leaf are (*i*) cuticle feebly developed; (*ii*) stomata restricted to upper epidermis ; (*iii*) presence of mucilage glands on the lower epidermis ; (*iv*) presence of large air-spaces in the xylem and greater development of phloem.

The sclereids give strength to the leaf and are thick-walled cells.

Leaf of Nerium. It is a dorsiventral leaf and a vertical section (Fig. 15.1) through it reveals the following arrangement of tissues :—

Epidermis. There are two layers of epidermises—the upper epidermis and the lower epidermis. The upper epidermis is made up of three layers of compactly arranged thin-walled cells. Some regard the lower two layers as hypodermis. The upper layer of epidermis is covered with a thick cuticle. The lower epidermis is also multi-layered. Usually, it consists of three layers. The lowest layer is covered with cuticle. The stomata are confined to the lower epidermis and are sunk in deep depressions formed by the incurving of the epidermis. These depressions or cavities are lined with numerous unicellular hair, which are direct prolongations of the epidermal cells. These hair are said to reduce the rate of transpiration because they surround the stomata and thus prevent the dry currents of air to strike against the stomata. These hair serve to protect the leaves against the injurious effect of heat, light and cold. The stomata are slightly elevated above the level of the pit epidermis.

Mesophyll. The mesophyll is distinguished into palisade parenchyma and spongy parenchyma. The palisade tissue consists of one to four layers of elongated chlorenchymatous cells. They are generally found below the upper epidermis, but may also occur next to lower epidermis (Fig. 15.1).

The spongy parenchyma is composed of loosely-arranged thin-walled cells so that there are large air-spaces. These cells also contain chloroplasts.

Vascular System. The mid-rib portion has a well-developed vascular bundle with phloem towards the lower epidermis and xylem towards the upper epidermis. The xylem consists of metaxylem next to the phloem and protoxylem towards the upper side. The vascular bundles of the veins are scattered in the lamina and consist of phloem and xylem.

Thick cuticle, multiple epidermis, stomata in pits, presence of epidermal hair in stomatal pits, and several-layered palisade are the xerophytic characters of the leaf.

Leaf of Salsola kali-tenuifolia. It is a succulent xerophytic leaf [Fig. 15.15], belonging to family *chenopodiaceae*.

Epidermis. It is composed of a single layer of thin-walled cells covered by a thin cuticle. The dorsiventrality of the leaf is exhibited

by the vascular bundle, which possesses phloem towards the lower side and xylem towards the upper side.

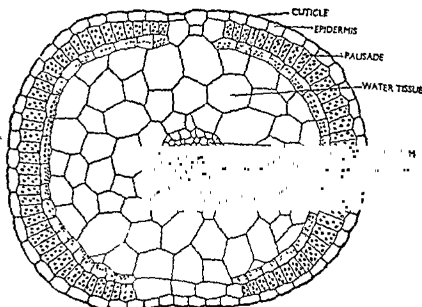


Fig. 15.15 T.S. through leaf of *Salsola kali-tenuifolia* illustrating peripheral palisade chlorenchyma and central water tissue

Mesophyll. It is differentiated into a peripheral palisade layer and a centrally located zone of thin-walled and compactly arranged large cells, which store water. They represent the water storage tissue. The palisade cells are relatively less elongated and contain chloroplasts. Its continuity is interrupted at two places (Fig. 15.15).

Vascular Region. It consists of a single vascular bundle with a distinction into phloem and xylem. Phloem faces the lower side.

Leaf of Portulaca oleracea. It is also a succulent xerophytic leaf (Fig. 15.16) and reveals a characteristic arrangement of chlorenchymatous cells. The epidermis is two-layer thick. The inner layer is of large thin-walled cells, which store water. The figure shows a section (T.S.) through a portion of the leaf passing through a small vein. The palisade cells are arranged in a ring round the vein. These cells are elongated and contain numerous scattered chloroplasts. Next to this is the layer of large funnel-shaped cells, which closely surround the vascular bundle of the vein. These cells contain chloroplasts that are aggregated at the bases of the cells and are not scattered. The vascular bundle shows no distinction into xylem and phloem and is poorly developed. It is a dicot leaf (*portulacaceae*).

Leaf of Mango (*Mangifera indica.* Anacardiaceae, Dicot). A vertical section of the leaf reveals the following structures (Fig. 15.17).

Epidermis. Both the upper and the lower epidermal layers are uniseriate and are composed of compactly arranged tabular cells. The upper epidermis is covered with a comparatively thick layer of cuticle

and lacks stomata. The lower epidermis is perforated by stomata and has a thinner cuticle.

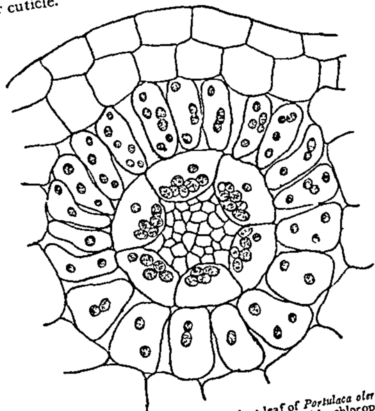


Fig. 15.16. T.S. portion of succulent leaf of *Portulaca oleracea*, showing a festoon of funnel-shaped cells with chloroplasts grouped at the base, surrounding a vein and an outer ring of palisade cells with scattered chloroplasts.

Mesophyll. It is clearly distinguishable into palisade tissue and spongy parenchyma. The palisade tissue is composed of elongated cells arranged regularly in two layers below the upper epidermis. The cells contain chloroplasts. The palisade forms a continuous layer except at places above the larger vascular bundles, where its place is taken by cells of bundle-sheath extension. These cells are arranged at plane at right angles to the upper epidermis. The chloroplasts are distributed along the radial walls of cells. The cells of the spongy parenchyma are loosely arranged and enclose small air-spaces. These cells also contain chloroplasts. The number of chloroplasts is comparatively less than the palisade cells.

Vascular Region. It consists of a large number of small and large vascular bundles. The bundles are collateral and closed and are enclosed by a parenchymatous sheath, which is quite separate from the epidermal layers in the case of smaller vascular bundles. In the larger bundles, the bundle-sheath is in contact with epidermal layers through bundle-sheath extensions, which consist of thin-walled chlorophylless

cells. Sometimes, the cells of the bundle-sheath extension possess cellulose thickenings. The phloem consists of sieve-tubes, companion

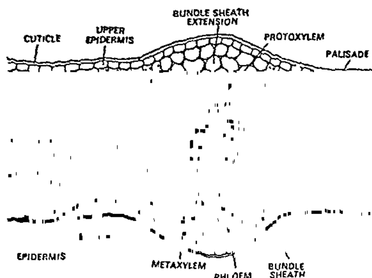


Fig. 15.17. T.S. of leaf of *Mangifera indica* (Mango).

cells, a little phloem parenchyma is present towards the lower epidermis. The xylem consists of metaxylem and protoxylem vessels and faces, the upper epidermis. The xylem consists of vessels and xylem parenchyma. Tracheids and fibres are absent.

Leaf of Banyan (*Ficus benghalensis, Moraceae,* Dicot). A vertical section through the dorsivental leaf of *Ficus benghalensis* reveals certain interesting peculiarities (Fig. 15.13).

Epidermis. It consists of two layers, the upper epidermis and the lower epidermis. Both of them are multiseriate. In the upper epidermis, the outermost layer is made up (at maturity) of smaller cells and is covered by thick cuticle. The cells of outer layer divide tangentially to give rise to the lower two layers, whose cells are comparatively large in size. Here and there, there are larger cells below the outer layer of the epidermis. These cells are called the lithocytes and contain a cluster of crystals of calcium carbonate. These clusters are called cystoliths and are attached to the roof of the lithocytes by a distinct stalk. The lower epidermis is also three-layered and is covered by a cuticle. The stomata occur only on the lower epidermis and are sunk.

Mesophyll. It consists of two or more layers of compactly arranged columnar cells that contain chloroplasts and form the palisade tissue of the leaf. It is the chief photosynthetic region. The spongy parenchyma consists of loosely arranged cells. The intercellular spaces are small. The cells contain chloroplasts. The palisade tissue is interrupted above the larger vascular bundles by the cells of bundle-sheath extension.

Vascular System. It is similar to that of *Magnifera indica* (Mango) except that in the larger vascular bundles there are present scleren-

chyma patches next to xylem and below phloem. The patches are absent in smaller vascular bundles (Fig. 15.13).

Leaf of calotropis procera (Fig. 15.18). The leaf is xerophytic. The epidermis is covered with thick cuticle. Grains of wax are present

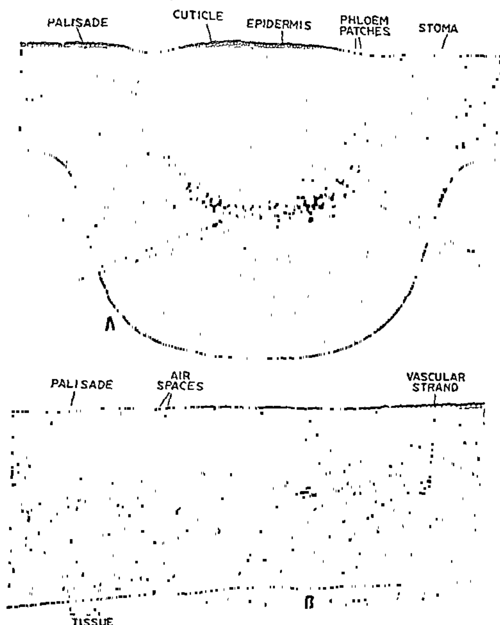


Fig. 15.18 (A—B). T.S. Leaf of *Calotropis procera*. (AB) A, T.S. through mid-rib portion, B, T.S. through a portions of lamina.

on the cuticle. The stomata are present on both the upper and the lower epidermises. Latex cells are also present in the mid-rib region

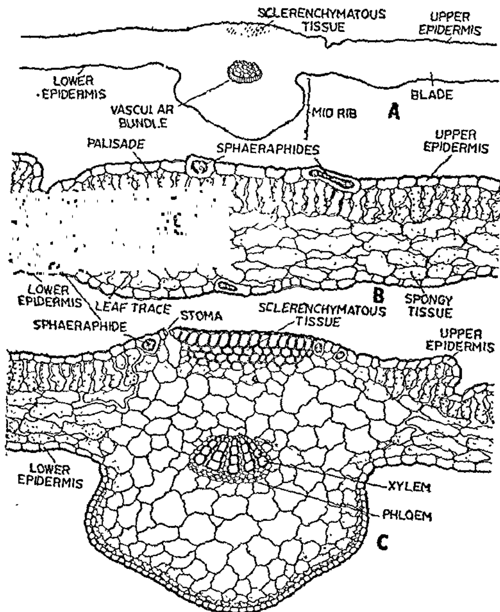


Fig. 15.19. (A—C). T.S. through leaf of *Polygonum barbatum*. A, outline diagram B, section passing through a portion of lamina. C, section passing through the mid-rib.

Note that the stomata are restrided to the upper epidermis. The vascular elements are less developed in the mid-rib region. Sclerenchymatous tissue is present below the upper epidermis in the mid-rib region. Also note the sphaeraphides in epidermis.

and mesophyll. The palisade consists of two or three layers of loosely arranged palisade cells. The cells of spongy parenchyma are lobed and loosely arranged to enclose large air-spaces. They contain abundant chloroplasts. The cells in the mid-rib region are closely packed. The

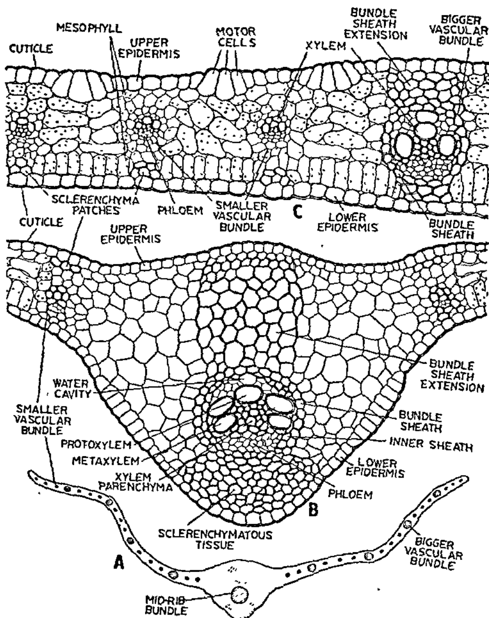


Fig. 15.20 (A—C). T.S. leaf of *Triticum aestivum*,
A, Outline diagram T.S. of whole leaf.
B, T.S. through mid-rib region. C, T.S. through lamina.

for the rolling of the leaves in dry weather. In water plants like *Potamogeton*, the cells of the upper and lower epidermises contain chloroplasts. In the leaves of *Maranta* and *Asarum canadense*, the outer walls of the cells in upper epidermis are convex and show prominent bulges. They are supposed to converge the rays of incident light. In *Fittonia*, isolated cells in the upper epidermis, known as *ocellae*, are more papillate than their neighbouring cells. Stomata are found on both

the upper and the lower epidermises. In water-plants, they are restricted only to the upper surface. In some grasses such as *Ammophilla arenaria* and *Poa pratensis*, the stomata are found only on the upper epidermis. The epidermal cells in many grasses are impregnated with silica. The epidermal cells also bear hair, which are generally unicelluar in the grasses. In *Agave americana* the cells in upper epidermis are covered by a layer of wax, cuticle, and a cellulose layer (Fig. 3.5, p. 63).

Mesophyll. This tissue lies between the two layers of epidermis. In the isobilateral leaves of monocotyledons, the mesophyll either lacks

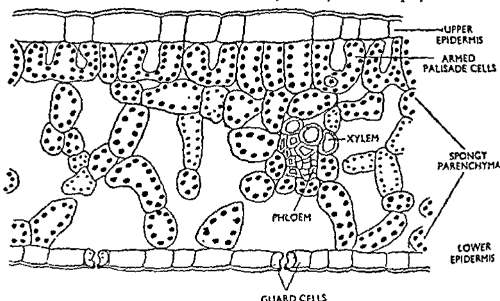


Fig. 15 21. V S. through leaf of *Lilium* sp. (Monocot) showing detailed internal structure. Note the armed palisade cells.

differentiation into spongy tissue and palisade tissue (Maize) or, if there is a distinction, the palisade is found on both the upper and the lower sides. In maize, the mesophyll is composed of similar types of cells which appear more or less rounded in a transverse section and enclose lots of intercellular spaces. The cells contain chloroplasts. The intercellular spaces form a continuous communicating system connected to the external environments through the substomatal cavities and stomata. In th[illegible] *Ammophila arenaria,* there is a well-developed sclerechyma that [illegible] ridges and is connected with vasc[illegible] sts of compactly arranged chlorenchymatous [illegible] of non-chlorenchymatous cells [illegible] the lower epidermis. These cells are also compactly arranged.
[illegible] there is a distinct layer of palisade
[illegible] below the
[illegible] ntral.
[illegible] lisade
[illegible] bular
parenchyma is made up [illegible] along
leaves of *Allium cepa,* the palisade is found [illegible] along the entire circumference of the leaf. Next to it is the spongy parenchyma.

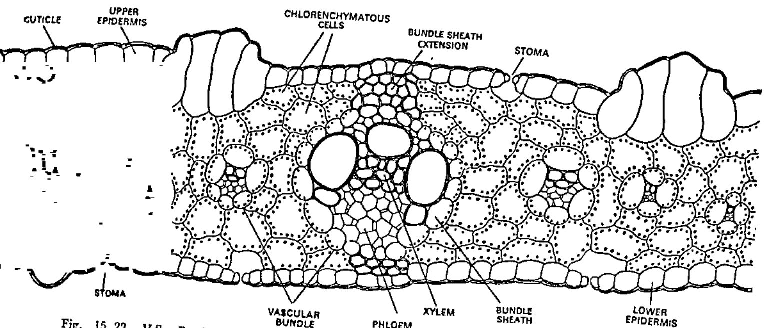


Fig. 15. 22. V.S. Portion of lamina of *Zea mays* leaf, showing detailed internal structure. Note the large motor or bulliform cells in the epidermis.

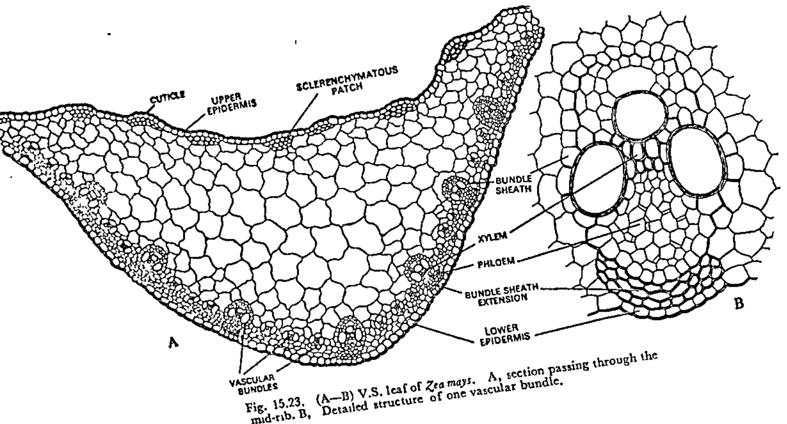


Fig. 15.23. (A—B) V.S. leaf of *Zea mays*. A, section passing through the mid-rib. B, Detailed structure of one vascular bundle.

Vascular System. In maize the median portion of lamina is thickened on the adaxial side and has a number of conjoint and collateral vascular bundles. In the rest of the lamina (on either side of the mid-rib) the vascular bundles of various sizes alternate with one another. The vascular bundles are surrounded by a definite bundle-sheath. In some cases the bundle-sheath is connected with upper and lower epidermises by groups of compact cells called the bundle-sheath extension (Fig. 15.20). In maize, these bundle-sheath extensions are sclerechymatous. In some cases (Fig 15.23), the vascular bundles have a sclerenchymatous cap of several layers. The phloem is generally towards the lower epidermis and xylem towards the upper side. In *Iris*, the vascular bundles, as seen in a transverse section, appear to be in a single file. Half of the bundles have phloem towards the upper epidermis and xylem towards the lower side and the rest half have phloem towards the lower side and xylem towards the upper side. In *Ammophila arenaria*, the vascular bundles are present below the ridges and possess xylem towards the upper side and phloem towards the lower side. Each vascular bundle has a distinct endodermis (bundle-sheath), which is connected with the upper epidermis by a sclerenchymatous tissue. The elements composing the xylem and phloem are similar to those of the dicotyledonous leaves and stems. In *Triticum* (Fig. 15.20), the vascular bundles in the veins are surrounded by two bundle-sheaths, the outer layer of bundle-sheath is made up of parenchyma cells, and the inner layer of bundle-sheath is made up of thick-walled cells. Such grasses are known as *festucoid grasses*. In maize, there is only one layer of bundle-sheath and such grasses are called *panicoid grasses*. In *Musa sapientum*, the vascular bundles are accompanied by laticifers (Fig. 15.29), that are unbranched.

Types of Leaves (Fig. 15.24. A—F). Anatomically, the leaves can be classified as under :—

(*i*) *Bifacial leaves* These leaves have upper and lower epidermal layers. The palisade tissue is confined either below the upper epidermis (*e.g.*, *Prunus*, *Nerium* etc.) or next to lower epidermis *e.g.*, *Allium ursinum*. The latter type is called *inverted bifacial* (Fig. 15.21 B) leaf.

(*ii*) *Unifacial leaves*. There is no distinction into upper and lower epidermises. To this category belong the cylindrical leaves of onion (Fig. 15.30) and *Juncus*. In *Iris* the leaf is unificial and flattened.

(*iii*) *Equifacial* or *Isobilateral leaves*. In such leaves (Figs. 15.24 E,) the palisade is present next to both epidermal layers or there is no distinction into palisade and spongy tissue *e.g.*, Maize and other monocots.

(*iv*) *Albescent leaves* . In such leaves, palisade is confined to one half of the leaf *e.g.*, *Abutilon* (Fig. 15.6).

DESCRIPTIONS OF SOME MONOCOT LEAVES

Leaf of Molinia (Graminae). It is an example of a leaf of marshy plant which combines the characters of both the hydrophytes and the

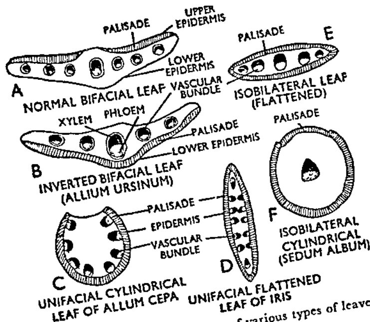


Fig. 15 24 Outline sketches of various types of leaves, (For explanation see text).

xerophytes. It is a dorsiventral leaf with its upper surface curved inwards. A vertical section of the leaf (Fig. 15.25) reveals the following structures :—

Epidermis. There are lower and upper epidermal layers. Both are composed of thin-walled cells that are compactly arranged. Both

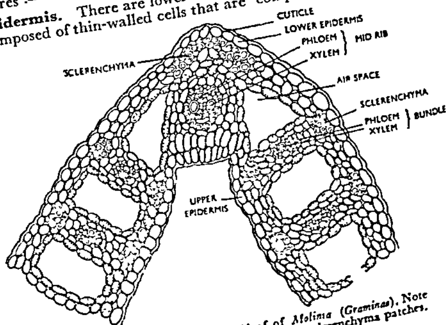


Fig. 15.25. V.S. portion of leaf of *Molinia* (*Gramineae*). Note the well-developed air-spaces as well as sclerenchyma patches.

the sides are covered with a cuticle. Due to infolding of the leaf at its upper surface the upper epidermis shows a distinct and characteristic depression (Fig. 15.25), where the epidermal cells are bigger in size and are turgescent. These cells are called the motor cells and loss of water from them is responsible for the curving inwards of the leaf. Just opposite to the depression on the upper side is a corresponding and distinct cone- like extension of the lower surface, forming a distinct obtuse angle.

Sclerenchyma. Sclerenchymatous patches are found both below the upper epidermis and next to the lower epidermis. They are opposite to each other and alternate with big air spaces in the mesophyll *i.e.*, they are present in the partitions of the air chambers at a position just below the epidermal layers The region of the partitions between the two sclerenchyma patches is occupied by parenchyma with a vascular bundle in the centre. The sclerenchyma patch next to the lower epidermis faces the motor cells in the upper epidermis in the region of the mid-rib.

Mesophyll. It is conspicuous by the presence of large air-chambers. The inner cells bordering the air-chambers contain chloroplasts. The cells next to upper epidermis also contain chloroplasts but are not elongated.

Vascular Region. There is a big vascular bundle in the centre with phloem towards lower epidermis and xylem towards upper side. It has distinct xylem and phloem elements. Many small vascular bundles are present in the partitions between the air-chambers. Bundle-sheath is made up of parenchyma cells.

Presence of sclerenchyma patches and motor cells is the xerophytic feature.

Leaf of Agave. The leaf of *Agave americana* (Fig. 15.26) is isobilateral because the palisade layer is found on both the surfaces of the leaf. A vertical section shows the following types and arrangement of the tissues :—

Epidermis. Both the upper and the lower epidermises are made up of a single layer of cells. The outer walls of the cells are covered with a thick cellulose layer. This layer is again covered with a thick cuticular layer that wedges into the cellulose layer in the radial walls of the cells (Fig. 15.26). Next to this is the cuticle which is again covered with a layer of wax grains. This type of thickening is found on both the epidermal layers. The stomata are found on both the upper and lower epidermal layers and are sunken. The subsidiary cells have projecting ridges and partially enclose the pit. The cuticle extends into the pit-cavity.

Mesophyll. The mesophyll consists of palisade parenchyma below the upper epidermis and next to the lower epidermis. The cells are thin-walled, elongated and chlorenchymatous. There are two layers of such cells. In-between the plalisade layers is the spongy parenchyma composed of loosely arranged thin-walled cells that enclose intercellular spaces.

Vascular region. It consists of several small and large vascular bundles that are capped on upper and lower ends by well-developed sclerenchymatous sheaths. The phloem is towards the lower epidermis and the xylem towards the upper surface. Vascular elements are well-developed.

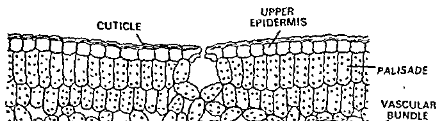


Fig. 15.26. V.S. leaf of *Agave americana* (xerophytic).

Prese ... sunken s ... bundles ... leaf and its spinous apex are the chief morphological features, which stamp it as a xerophytic plant.

Leaf of Phoenix sylvestis (Palmae, Monocot). It is a xerophytic and isobilateral leaf. A vertical section (Fig. 15.27) reveals the following structures :

Epidermis. The lower and upper epidermal layers are covered with thick cuticle and are composed of compactly arranged, thin-walled cells. Stomata are found on both the surfaces. A *single* layer of thin-walled sub-epidermal cells is present next to both the epidermal layers. Groups of large cells, called *motor cells*, are present.

Mesophyll. It is undifferentiated and consists of polygonal cells that enclose only small intercellular spaces. The cells contain chloroplasts.

Sclerenchyma. It is found in the form of patches of thick-walled cells next to both upper and lower epidermises. It gives rigidity to the leaf.

Vascular region. A number of small and large bundles alternate with each other. The large bundles are enclosed in sclerenchymatous sheath, which is continuous with the sclenchymatous patches above and below. The smaller bundles have a parenchymatous sheath. Each bundle has phloem towards the lower epidermis and xylem towards the upper side.

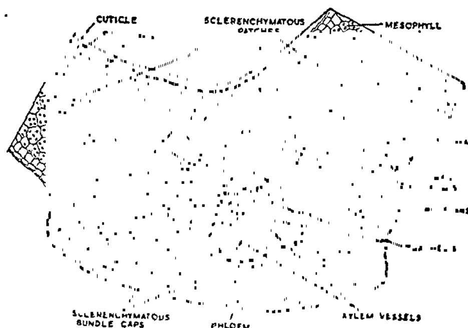


Fig. 15.27. V.S portion of leaf of *Phoenix dactylifera* (monocot) showing detailed internal structure. Note the **motor cells** and bands of sclerenchyma next to both the epidermal layers. The vascular bundle is capped on either side by extensively developed bundle caps.

Presence of thick-walled patches next to the epidermal layers, presence of motor cells and presence of sclerenchymatous caps on either side of the vascular bundles are the xerophytic characters.

Leaf of Maize (Zea mays). *Zea mays* belongs to family Graminae (Monocot). It is an isobilateral leaf. A vertical section reveals the following characteristics (Fig. 15.22) :—

Epidermis. There is an upper and a lower layer of epidermis. Both the layers are composed of a single layer of cells and possess stomata. Some of the cells in the upper epidermis are large in size and are called motor cells. They occur in groups and are fully turgid. They are also known as bulliform cells. The epidermal cells are covered by a thick cuticle.

Mesophyll. The mesophyll is not differentiated into palisade and spongy parenchyma. The cells are almost spherical and enclose small inter-cellular spaces. The cells contain chloroplasts.

Vascular system. It consists of a number of large and small vascular bundles. Each bundle is surrounded by a layer of thin-walled

cells, called the bundle sheath. The cells contain starch. The large bundles have prominent sclerenchyma patches on both the upper and the lower ends. They extend between the bundles and epidermal layers. The larger bundles have a distinct phloem towards the lower epidermis and xylem towards the upper epidermis. The phloem has sieve-tubes and companion cells. The xylem consists of two pitted metaxylem vessels that are oval in shape. In-between them, tracheids are also present. Xylem parenchyma is scanty. Protoxylem is represented by a lysigenous cavity, which faces the upper epidermis.

The smaller bundles are also surrounded by individual sheaths and contain phloem and xylem. Both the tissues are distinct but less developed. The bundles are conjoint, collateral and closed.

The thick cuticle, sclerenchyma patches and motor cells are the xerophytic features of the leaf.

Leaf of Triticum vulgare. It is also an isobilateral leaf with conspicuous ridges and furrows on the upper epidermis. A vertical section (Fig. 15.20) reveals the following tissues :—

Epidermis. It consists of two layers : the upper epidermis and the lower epidermis. They are uniseriate and are composed of more or less oval cells. Some of the cells in the upper epidermis are distended and larger in size. These are called the motor cells or bulliform cells. They occur in groups. A layer of cuticle covers both the epidermal layers. Stomata are found on both the surfaces. The upper epidermal shows distinct ridges and furrows. The bulliform or motor cells are found in the furrows alone. The surface of the leaf is rough due to the presence of grains of silica. The motor cells are said to be involved in the involution and folding of the leaves but some studies (Sheilds, 1951) have shown that shrinkage of other tissues is also equally responsible for this.

Sclerenchyma. It occurs in the form of patches below the upper epidermis and next to the lower epidermis. It gives rigidity to the leaf.

Mesophyll There is not much demarcation between the palisade cells and spongy parenchyma. In this case the cells of the mesophyll beneath the upper epidermis and next to lower epidermis are regularly arranged and are a little longer. The cells in the centre are more or less oval and are irregularly arranged with intercellular spaces between them.

Vascular Region. The vascular bundles are of different sizes and alternate regularly with one another. The central bundle is the largest. Each vascular bundle is surrounded by a double sheath (Festucoid grasses). The outer layer of sheath is composed of thin-walled cells. The inner layer is made up of thick-walled cells. Brown (1958) classified grasses into Festucoid with double bundle-sheath and Panicoid (maize) with single-layered sheath. The larger vascular bundles are associated with the sub-epidermal fibre-plates or sclerenchyma patches next to the epidermal layers. The smaller bundles have no such contacts with the sub-epidermal patches. The bundles are conjoint, collateral, and closed. The phloem is towards the lower epidermis and xylem towards the upper side.

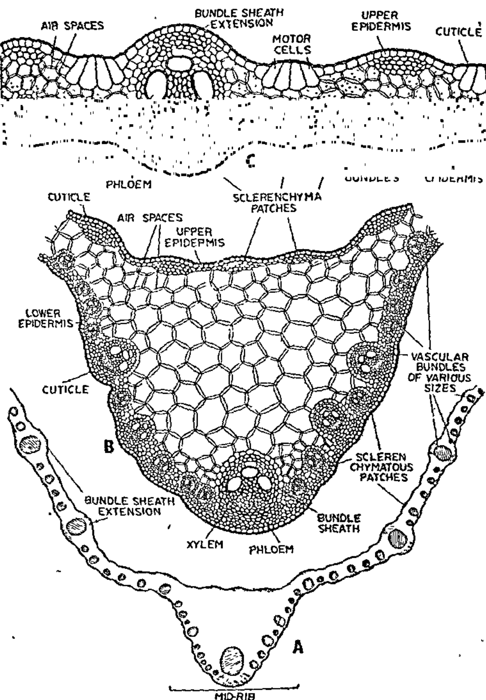


Fig. 15.28 (A—C). T.S. leaf of *Oriza sativa*.
A, Outline diagram. B, T.S. through mid-rib portion.
C, T.S. through part of lamina.

Presence of thick-walled patches next to the epidermal layers, and presence of motor cells are xerophytic characters of this leaf.

Leaf of *Oriza sativa* (Fig. 15.28) also shows a similar structure.

Leaf of Musa sapientum (Banana, Musaceae, Monocot). This is an example of a dorsiventral monocot leaf (Fig. 15.29) and reveals the followidg structures in a vertical section.

Epidermis. It consists, as usual, of upper and lower epidermal layers. Both are uniseriate and consist of closely packed, thin-walled cells that are covered by a layer of cuticle which is more prominent and well-developed in the upper epidermis. Stomata are restricted only to the lower epidermis. A layer of large cells is present below the upper epidermis and next to the lower epidermis. These cells are colourless and appear to store water.

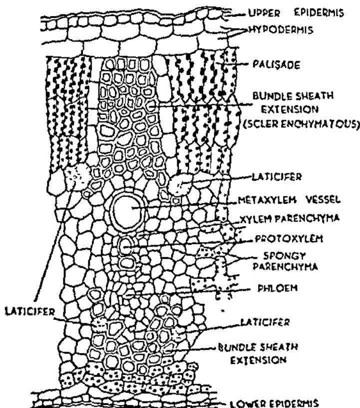


Fig. 15.29. *Musa sapientum.* T.S. portion of leaf (Monocot) showing *dorsiventral structure and laticifers accompanying the vascular bundles.*

Mesophyll. It is distinguished into a palisade tissue and spongy [illegible] two layers of columnar cells, [illegible] arranged along the radial [illegible] layer is interrupted by the presence of sclerenchyma patches above the vascular bundles. The spongy parenchyma region is traversed by a number of large air-spaces that alternate with the vascular bundles. The spongy parenchyma cells that are present next to the lower epidermis are almost rounded and contain chloroplasts. Sclerenchyma patches are present next to the lower epidermis at places where vascular bundles are present.

The air-spaces in this leaf develop lysigenously.

Vascular Region. It consists of a number of oval vascular bundles. The phloem is towards the lower epidermis and xylem towards the upper epidermis. Each bundle is surrounded by a parenchymatous sheath and is capped by sclerenchyma patches on both the ends.

Leaf of Onion (*Allium cepa*. Alliaceae, Monocot). It is an example of a cylindrical leaf that appears more or less circular in a cross-section. It is not dorsiventral and shows no distinction into distinct epidermal layers. A cross section of the leaf (Fig. 15.30) reveals the following structures :—

Epidermis. It forms a continuous uniseriate layer of small and closely-packed parenchymatous cells all around the circular contour of the leaf. Stomata are present all around the epidermal surface and slightly below the level. Cuticle is well-developed.

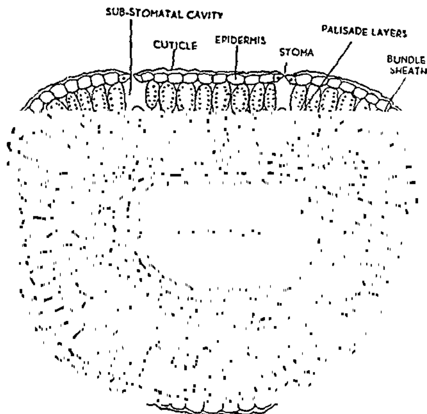


Fig. 15.30. T.S. leaf (cylindrical) of Onion (*Allium cepa, Alliaceae.*)

Mesophyll. It is differentiated into palisade tissue and spongy parenchyma. The palisade tissue forms a continuous layer of columnar cells arranged in two layers below the epidermis. These contain abundant chloroplasts. The spongy parenchyma cells are almost elliptical or roughly oval and contain chloroplasts. They are loosely arranged and enclose small intercellular spaces. Next to the spongy

Leaf of *Oriza sativa* (Fig
Leaf of Musa sapienti
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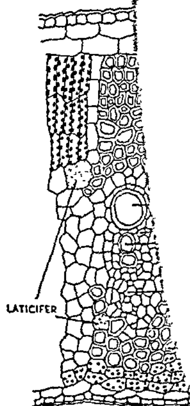


Fig. 15.29. *Musa sapientum.* T.S. po
dorsiventral structure and laticifers acc

Mesophyll. It is distinguished into
parenchyma. The palisade consists of t
which are filled with chloroplasts that are
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presence of sclerenchyma patches above the
spongy parenchyma region is traversed by a n
that alternate with the vascular bundles. The s
that are present next to the lower epidermis are
contain chloroplasts. Sclerenchyma patches are
lower epidermis at places where vascular bundles a

parenchyma is a single layer of almost barrel-shaped cells which lack chloroplasts. This layer forms the boundary of the large central cavity.

Vascular Region. It consists of a varying number of conjoint, collateral, and closed vascular bundles that are arranged in a circle below the palisade and among the spongy parenchymatous tissue. Each bundle is surrounded by a single-layered parenchymatous bundle-sheath. The phloem is always directed towards the lower epidermis and xylem towards the upper epidermis.

Leaf of Typha (Figs. 15.31 to 15.36). *Typha* is a common amphibious plant that shows mingling of hydrophytic and xerophytic characters in its leaves. The leaf appears semicircular in outline in a transverse section (Fig. 15.30). It reveals the following structures.

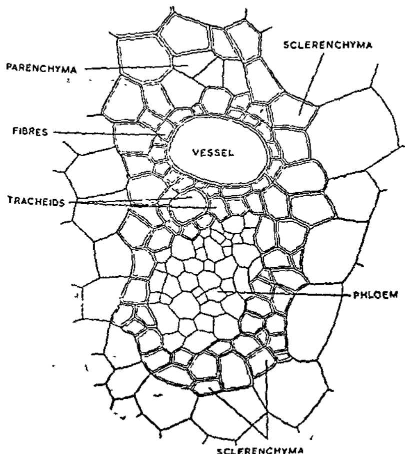


Fig. 15.32. Leaf of *Typha*. A. vascular bundle from the partition, showing detailed structure. It has one large xylem vessel.

Epidermis. It is composed of a single layer of thin-walled cells and is perforated by stomata all around. It is covered by a thick cuticle.

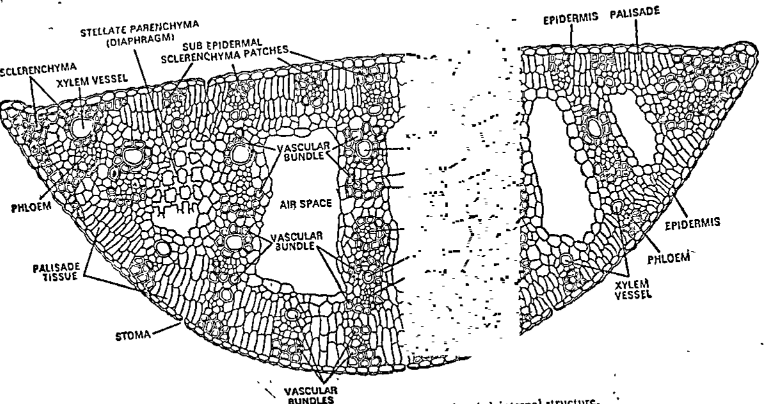


Fig. 15.31. V.S. leaf of *Typha*, showing detailed internal structure.

parenchyma is a single layer of almost barrel-shaped cells which lack chloroplasts. This layer forms the boundary of the large central cavity.

Vascular Region. It consists of a varying number of conjoint, collateral, and closed vascular bundles that are arranged in a circle below the palisade and among the spongy parenchymatous tissue. Each bundle is surrounded by a single-layered parenchymatous bundle-sheath. The phloem is always directed towards the lower epidermis and xylem towards the upper epidermis.

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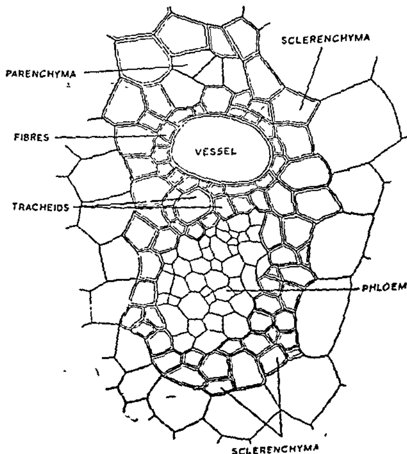


Fig. 15.32. Leaf of *Typha*. A. vascular bundle from the partition, showing detailed structure. It has one large xylem vessel.

Epidermis. It is composed of a single layer of thin-walled cells and is perforated by stomata all around. It is covered by a thick cuticle.

Below the epidermis there are small and large patches of sclerenchymatous cells (Fig. 15.30). These patches form bundle-caps over the sub-epidermal vascular bundles.

Mesophyll. The mesophyll is distinguished into *palisade parenchyma* and *spongy parenchyma.* The palisade cells occur in three to many layers of elongated chlorenchymatous cells (Fig. 15.35). It is absent at the corners (Fig. 15.36). The palisade is present in patches interrupted by sclerenchymatous patches and sub-epidermal vascular bundles (Fig. 15.30). These alternating patches of palisade and sclerenchyma are present all round the leaf so that the leaf is *isobilateral.*

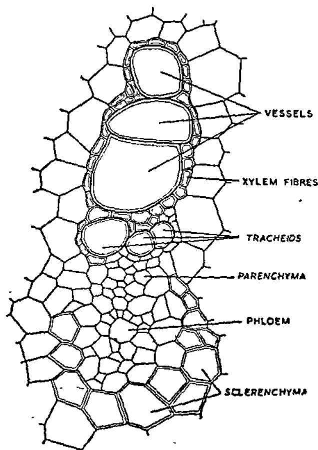


Fig. 15.33. Leaf of *Typha*. A vascular bundle from the partition showing three xylem vessels.

The spongy parenchyma is traversed by large intercellular spaces separated by many layered partition walls (15.31). Each large air-space is traversed at intervals by diaphragms made up of stellate parenchyma (Fig. 15.31). The margins of the leaf are occupied by a well-developed sclerenchymatous patch (Fig. 15.36).

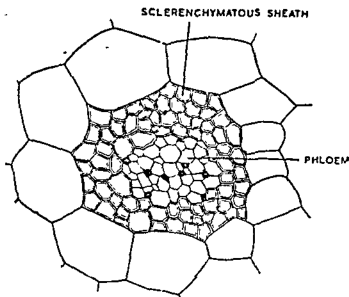


Fig. 15.34. Leaf of *Typha*. A phloem bundle from the partition. It is surrounded by a sclerenchymatous sheath.

SCLERENCHYMATOUS PATCH
CUTICLE
EPIDERMIS
PALISADE LAYERS
FIBRE CELLS
RACHEID
PHLOEM
SCLERENCHYMATOUS SHEATH

Fig. 15.35. T.S. Leaf of *Typha* passing through a portion of the leaf showing epidermis, palisade, sclerenchymatous patch and a sub-epidermal vascular bundle.

Vascular Region. The leaf is parallel-veined and the following types of vascular bundles can be recognised :—

1. **Sub-epidermal Vascular bundles.** They are present at intervals below the sub-epidermal sclerenchymatous patch (Figs. 15.31 and 15.34). The xylem is next to the sclerenchymatous patch and consists of vessels, tracheids and xylem fibres (Fig. 15.35). The phloem forms a patch below the xylem. The bundle is collateral and closed. Here and there, exclusively, xylem bundles can also be seen.

2. **Vascular bundles of Partition Walls.** Usually, three vascular bundles are present in each partition wall of the air-spaces (Figs. 15.31) These vascular bundles are developed in series, the central one being exclusively a phloem bundle (Fig. 15.34), the other two are collateral and closed. The phloem bundle is surrounded by a thick sclerenchymatous sheath.

The chief xerophytic characters of the leaf are :—

1. Presence of thick cuticle.
2. Presence of sub-epidermal sclerenchymatous patches.

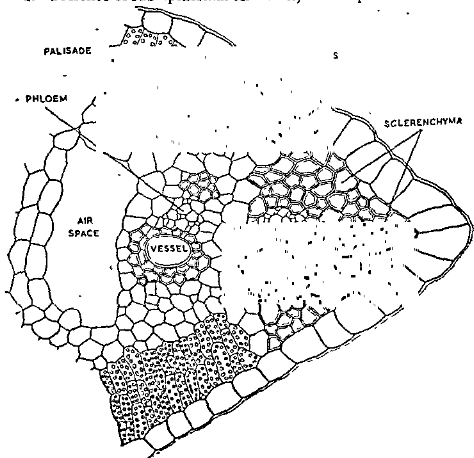


Fig. 15.36. T.S. leaf of *Typha* passing through the corner of lamina. Note the thick sclerenchymatous patch, two vascular bundles and an air-space.

3. Presence of sclerenchyma at the corners.
4. Many-layered palisade parenchyma.

The occurrence of large air-spaces is a hydrophytic character.

Leaf of Aloe (Fig. 15.37, 15.38). It is a succulent xerophytic leaf that stores copious amount of mucilage and water. The mucilage is stored in the large spongy parenchyma cells found in the centre of the leaf. The large and small vascular bundles form a peripheral ring around the central storage tissue. The bundles are conjoint and collateral. There is a well-developed palisade tissue below the epidermis. It is present all around the leaf so that the leaf is isobilateral. The epidermis is covered by a thick cuticle and is interrupted by sunken stomata. The thick cuticle is usually papillate and follows outline of the outer walls of epidermal cells. The cuticle forms a strong and well developed lobe on either side of the outer rim of suprastomatal cavity. The epidermal cells are usually broader than long and those of both surfaces similar. Epidermal cells at the leaf margin are longer than broad. The outer wall of epidermal cells bears papillae in all species of *Aloe* (D.F. Cutler, 1972). Inner and anticlinal walls of epidermal cells are often thickened. The sunken stomata have a suprastomatal cavity and a substomatal cavity. The former has parallel or overarching sides. Cuticular ledes are present in suprastomatal as well as sub-stomotal cavities. Palisade is several-layered thick and present on both the surfaces. Hypodermis is absent or present near the leaf apex of some species, where it is one layer below the adaxial surface (D.F. Cutler, 1972).

[illegible] boundary between pal[illegible] vascular bundles alte[illegible] wards and forms a distinct cap. Phloem has narrow sieve-tubes and companion cells.

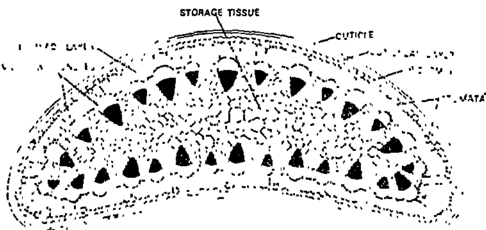


Fig. 15.37. T.S. leaf of Aloe, an outline diagram.

Xylem is composed of narrow tracheids, rarely wide. Tracheids are mostly spiral or annular; some wider tracheids exhibit opposite pitting.

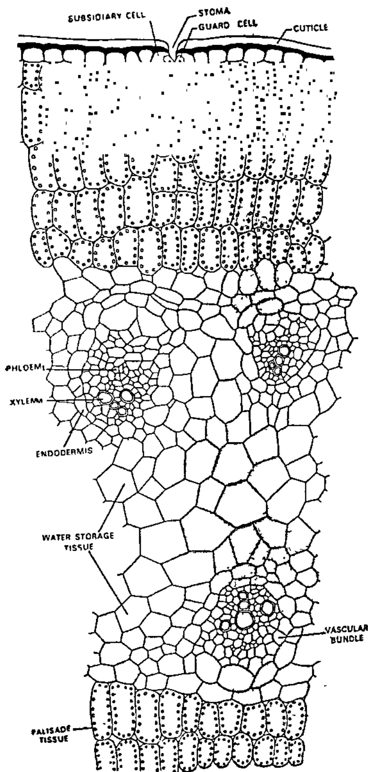


Fig. 15 38. T.S. portion of leaf of *Aloe*, showing detailed internal structure.

End-walls of tracheids are oblique. Endodermis or bundle sheath can be recognised around each vascular bundle and is very clear towards the phloem end.

The central tissue is composed of wide parenchmatous cells containing mucilaginous sap, often separated from palisade by distinct layers of narrower thin-walled cells.

Raphides are present in many species in sacs scattered among palisade cells. Tannins and silica bodies are absent.

Thick cuticle, sunken stomata, many-layered palisade and presence of mucilage containing cells in the central region are the xerophytic characters of the leaf.

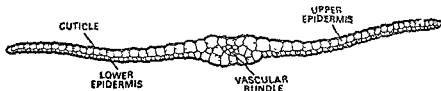


Fig. 15.39. T.S. leaf of *Hydrilla verticillata*. Note the absence of mesophyll and extremely reduced vascular region.

In the leaf of *Hydrilla* (Fig. 15.39) which is a submerged hydrophyte (Monocot), there is no mesophyll. The upper epidermis has longer cells whereas the lower epidermis has comparatively small cells. The cells contain abundant chloroplasts and are thus photosynthetic. The vascular region has undifferentiated vascular elements.

THE PETIOLE

Petiole is that part of the leaf which connects it with the stem and holds it in a position so as to expose it to adequate amount of light and air. In order to have a clear idea of the vasculature of petiole, which generally resembles that of a stem, sections should be cut at various levels of the petiole as it reveals variations in the arrangement of the vascular region. Usually, sections are cut at the distal end *i.e.*, immediately below the lamina. In order to compare the petiolar structure of the various leaves, sections should be cut at the same level. Metacalfe and Chalk have recognised eight general types of vasculature in the petioles of dicotyledons.

Petioles of a few common plants have been selected here to acquaint the student with their *structure*.

1. **Petiole of Cucurbita.** It has been selected to illustrate a type of petiole in which the bundles are bicollateral and arranged in a ring. The structure is exactly similar to that of the stem (Fig. 15.40 A). A transverse section shows the following tissues :—

Epidermis. It is composed of a single layer of compactly arranged parenchymatous cells. There is a well-developed cuticle. It is thrown into ridges and furrows. A number of multicellular hair arise from the epidermis.

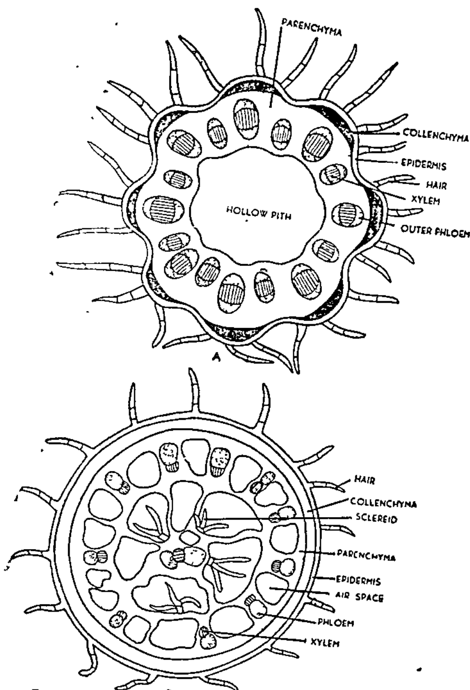


Fig. 15 40 A—B. A, T.S (diagrammatic) through the petiole of *Cucurbita*. B, T S. (diagrammatic) through the petiole of a water plant, *Nymphaea stellata*.

Ground Tissue or Cortex. It consists of collenchymatous patches below the ridges alone. The rest of the cortex is made up of parenchymatous cells, which enclose intercelluar spaces. The cells may also contain chloroplasts.

There is no endodermis and no pericycle. The central region is occupied by a large air-cavity.

Vascular Region. It consists of a number of large and small vascular bundles. The bundles are bicollateral and conjoint. The larger bundles are found below the ridges and smaller ones below the grooves. The bundles are arranged in a ring in the cortex or the ground tissue.

It is an example of a petiole with discrete bundles arranged in a ring.

2. **Petiole of Nymphaea stellata.** It illustrates the internal structure of an aquatic petiole (Fig. 15.40 B). The following structure is revealed by a transverse section :—

Epidermis. It is made up of a single layer of thin-walled cells that are compactly arranged and have thin cuticle. The cells contain chloroplasts. Multicellular hair arise from the epidermis.

Hypodermis. It is composed of two or more layers of collenchymatous cells and gives mechanical strength to the petiole so as to hold the leaf in position.

Ground tissue. It is full of large air-spaces. The vascular bundles are scattered in the ground tissue and are present in the partitions of the air-chambers. Presence of trichosclereids in the air-chambers is a characteristic feature. The sclereids are deposited with crystals of calcium oxalate.

Vascular System. It consists of scattered vascular bundles that are collateral and closed. The xylem is poorly developed and its elements break down to form small lacunae next to the phloem, which is well developed and consists of sieve-tubes and companion cells. Phloem parenchyma and fibres are absent. The vascular bundles with a patch of phloem on either side of the xylem lacuna are also found.

It is an example of a petiole with scattered vascular bundles.

3. **Petiole of Prunus persica.** There is a distinct petiolar groove, and a transverse section (Fig. 15.41 A) reveals a single layered [illegible] side and xylem towards the groove. It is an example of petiole in which the vascular system is represented by a single cup-shaped vascular bundle.

4. **Petiole of Eriobotrya japonica.** The outline in a cross-section (Fig. 15.41), is circular. There is a disinct epidermis followed by a ground tissue in which are found numerous scattered sclerenchyma strands. These are generally found around the vascular region which consists of a continuous circular cylinder of phloem surrounding a continuous cyclinder of xylem. There is a distinct pith

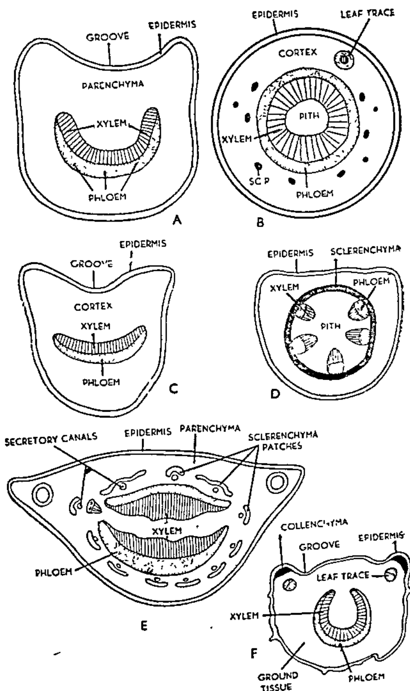


Fig. 15.41. A—F (All diagrammatic transverse sections). A, Petiole of *Prunus persica*. B, Petiole of *Eriobotrya japonica*. C, Petiole of *Galphimia gracilis*. D. Petiole of *Oxalis*. E. Petiole of *Mangifera indica*. F. Petiole of *Viola odorata*. Scp. Sclerenchyma patches.

in the centre. The stele resembles the ectophloic siphonostele. A leaf trace bundle is present.

5. **Petiole of Galphimia gracilis.** *Galphimia gracilis* is a common ornamental shrub with yellow flowers Its petiole is selected as an example because the vascular strand in this case (Fig. 15.41 C) is saucer-shaped and is continuous *i.e.*, not divided into discrete vascular bundles. There is a distinct petiolar groove. The phloem is towards the lower side and xylem towards the groove.

6. **Petiole of Oxalis corniculata.** It is a common annual herb. A transverse section (Fig. 15.41 D) reveals a distinct epidermis, a parenchymatous cortex and a continuous cylinder of sclerenchyma. Next to this is a ring of discrete vascular bundles with xylem pointing towards the pith. There is a distinct pith in the centre.

7. **Petiole of Mangifera indica** (Mango). A transverse section at the distal end of the petiole (Fig. 15.41 E) reveals the following structure :—

Epidermis It is composed of a single layer of compactly arranged parenchymatous cells.

Ground Tissue. It consists of thin-walled cells. In it are scattered distinct strands of sclerenchyma. These strands are of various shapes (Fig. 15.41 E). Internal to each strand is a secretory canal.

Vascular System. It is represented by two large saucer-shaped bundles and a single small wedge-shaped bundle. The *large* stands face each other with their xylem pointing towards the centre and phloem outwards. Two leaf-trace bundles are found at the corners. The sclerenchyma strands and secretory canals are arranged in a ring round the vascular strands.

8. **Petiole of Viola odorata** (Banafsha). It is a common pot herb grown in the gardens for its blue flowers and green leaves. The petiole possesses a distinct groove with sub-epidermal collenchyma strands (Fig. 15.41 F) at the two angles. There are two leaf-trace bundles embedded in the ground tissue opposite to the angles. The single vascular strand is deep, cup-shaped or horse-shoe-shaped. Phloem is towards the outer side and xylem lining the cup. The cavity of the cup is occupied by parenchyma cells.

9. **Petiole of Nuphar luteum.** A cross-section (Fig. 15.42) through the petiole of *Nuphar luteum* shows a single-layered epidermis followed by a few layers of loosely arranged thin-walled sub-epidermal cells. The cortex is occupied by numerous air-spaces bordered by two-layer thick or one-layer thick partitions of parenchymatous cells. There is no endodermis and no pericycle. The vascular region is composed of many vascular bundles (only one is shown in the figure), each having a phloem towards the outer end and xylem represented by a large cavity towards the centre. In the petioles of *Nuphar* the air-cavities [illegible]

. but as they grow in age certain
e air-cavities and branch freely
mass of loosely-arranged

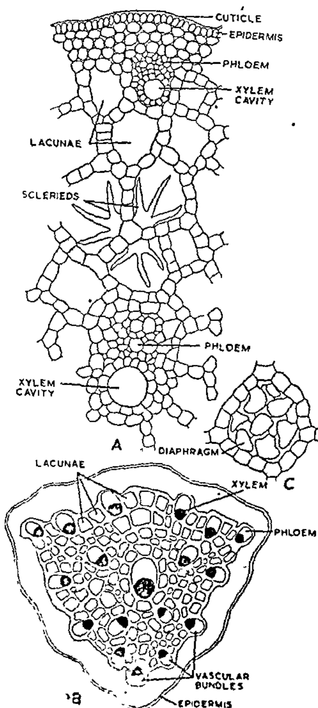


Fig. 15.42. (A—C). Petiole of *Nuphar lutea*. A, T.S. portion of petiole showing detailed internal structure. B, outline diagram of T.S. of petiole. C, A lacuna with diaphragm.

Sclerenchymatous idioblasts (sclereids) are present in the lacunae. These usually develop at the junctions of the three partition walls. They give mechanical strength to the petiole.

10. Petiole of Heptapleurum venulosum (Figs. 15.43, 15.44). The petiole shows an abnormal internal structure. It has two rings of vascular bundles. Bundles in the outer ring are of two types. There are larger bundles which almost regularly alternate with the smaller bundles. Both the smaller and larger bundles are collateral and endarch. Both are capped by a group of sclerenchymatous fibres, which are of the nature of substitute fibres and have greatly thickened and lignified walls. They have protoplasmic contents (Joshi, 1932). Towards the inner side of each large bundle, there is a resin canal (Fig. 15.43). The bundles of the inner ring are situated only opposite to the smaller bundles of the outer ring (Fig. 15.42). Their number, therefore, is only one half of that of the outer ring. The bundles of inner ring are inversely oriented *i.e.*, they have phloem towards the pith and xylem towards the outer side (Fig. 15.42). The internal bundles do not possess the fibrous cap. Bundles in both the rings possess cambium and are open.

The cortex of the petiole is characteristic in possessing two rings of resin canals (Fig. 15.43). One ring is present just below the epidermis. The other ring of canals is present just outside the external ring of

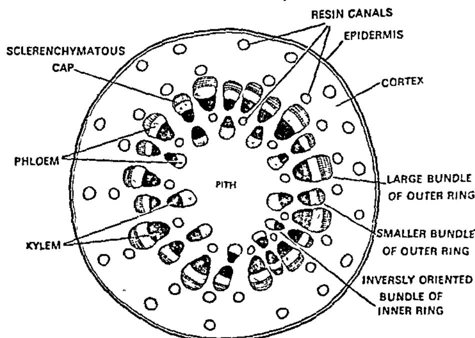
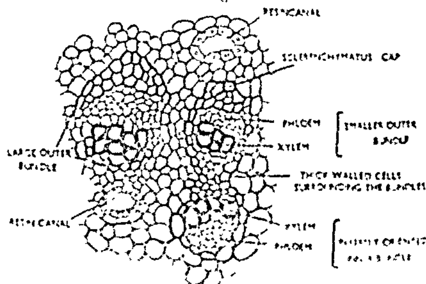


Fig. 15.43. T.S. petiole of *Heptapleurum venulosum* showing the arrangement of vascular bundles. The outer ring has large and small collateral bundles. The inner ring has inversely oriented bundles situated opposite to the smaller bundles of the outer ring.

vascular bundles. A third ring of canals is present internal to the larger bundles of the outer ring. The vascular bundles, at the base of the petiole, are scattered. Their arrangement in two rings is above the base.

Ontogenetic studies have revealed that the larger bundles of the outer ring begin to develop earlier and then later on in between them are formed the smaller bundles. The bundles of the inner ring develop simultaneously with those of the smaller bundles of the outer ring. All these bundles develop from separate procambial strands and their development follows a normal course. At a later stage, the cells surrounding the smaller bundles of the outer ring and those of the inner ring develop thick lignified walls and it appears as if both are surrounded by a common sheath (Fig. 15.43).



A transverse section of the phyllode shows xerophytic characteristics and reveals the following tissues :—

Epidermis. The epidermis is composed of a single layer of thin-walled cells. Its continuity is interrupted by the presence of stomata which are sunken. A well-developed cuticle is present.

Mesophyll. It is distinguishable into palisade tissue and spongy parenchyma composed of thin-walled and loosely arranged cells. The palisade tissue is composed of two layers of cells. Its continuity is interrupted by the presence of sclerenchymatous patches above and below the central vascular bundles. These patches are also found at the corners capping the corner bundles (Fig. 15.46).

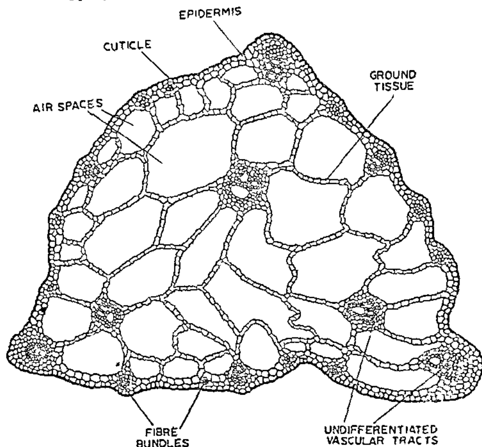


Fig. 15.45. T.S. Petiole of *Sagittaria sp.*

Vascular System. There are two big vascular bundles in the centre and one each at the corners. In addition, a number of vascular bundles are found next to the palisade tissue. The vascular bundles in the centre are completely surrounded by a sclerenchymatous sheath and possess well-developed phloem and xylem. The phloem in both of them faces [illegible] In the corner bundle, the [illegible] and almost surrounds the [illegible] on all sides except the xylem. The other smaller bundles also possess sclerenchymatous sheath.

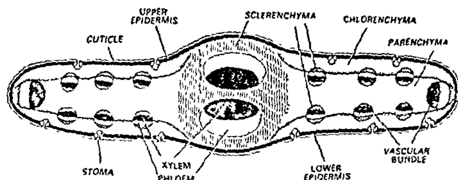


Fig 15 46 T.S. outline sketch of phyllode of Australian acacia. Note the mid-rib with two vascular bundles separated by sclerenchyma.

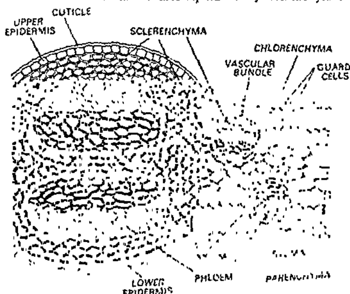


Fig. 15.47. (portion in detail) of phyllode of *Australian acacia* showing interanl structure.

ANATOMY OF LEGUMINOUS PULVINUS

Two characteristic features of the anatomy of pulvinus are (*i*) centralisation of the vascular tissue and the mechanical tissue ; (*ii*) the rigid-sclerenchyma of the pericycle is replaced by a flexible collenchyma. These two characters aid in the free bending movement of the leaf. Haberlandt (1928. p. 566), Watari (1934. p. 323) and Milanez (1972) have made detailed observations on the pulvinus of Leguminous plants (especially *Mimosa*) and confirmed the above two anatomical features. The collenchymtous cells of the pericycle are fusiform with pecto-cellulosic walls. The cortical cells are living and almost devoid of calcium oxalate crystals in *Mimosa* (*M. pudica, M. sensitiva, M. cylindrica*). The cells of the outer cortical layer are small, short and fusiform. They contain a few or many starch grains. Their walls are copiously pitted and contain abundant pectic substances.

In *Mimosa*, the petiole has six vascular bundles but, in the pulvinus, there are three such bundles because of the converging of three vascular strands to form a coherent mass. Later, they again divide into six.

16

DISTRIBUTION OF MECHANICAL TISSUE

Mechanical tissues. The mechanical tissues in small land plants and water plants are poorly developed. Large woody plants and their aerial organs are, however, subjected to considerable strain, and conspicuous mechanical tissues are present to ensure the maintenance of form and position. Haberlandt termed the mechanical tissue system as *stereome* and the cells composing them as *stereids.* The chief mechanical elements are: the *bast* and *wood fibres, collenchyma, sclerenchyma,* and the *turgid parenchymatous cells.* Thick-walled and cutinised epidermis also contributes to the rigidity of the plant. Occurrence of silica on the cell-walls in grasses also adds to the rigidity. In *Osmanthus,* the leaves possess T-shaped prop cells or the sclereides (Fig. 5.4, A), which give stiffness to the leaf. The *sclereids* or the stone cells generally occur as *idioblasts* and are usually scattered irregularly throughout the various tissues, as in barks of trees. More commonly, the mechanical elements are grouped into strands, the most usual condition being the association of mechanical and conductive elements, into a fibro-vascular bundle. Compact strands of bast fibres are commonly present outside the phloem. In the aerial stems of *Juncus baltiicus-litoralis* each vascular bundle is surrounded by a mechanical cylinder. In *Dianthus caryophyllus,* the entire vascular track is surrounded by a sclerenchymatous mechanical cylinder. The same is the case with the

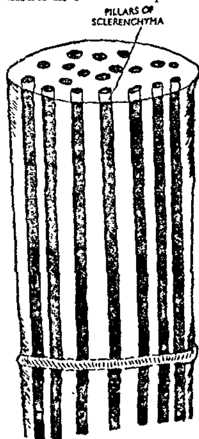


Fig. 16.1. The arrangement of mechanical tissue in monocots.

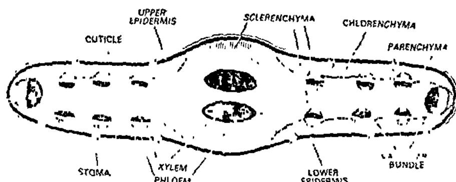
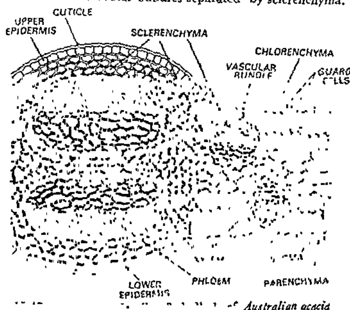


Fig. 15.46. T S. outline sketch of phyllode of Australian acacia. Note the mid-rib with two vascular bundles separated by sclerenchyma.



... *Australian acacia*

PULVINUS

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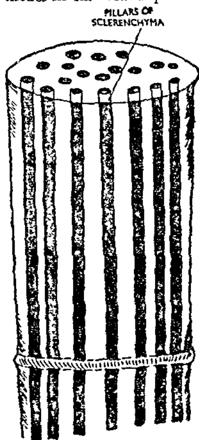


Fig. 16.1. The arrangement of mechanical tissue in monocots.

stems of the family *Cucurbitaceae*. The spiral arrangement of the microfibrils in the individual layer of the wall enhances the resistance to rupture of a sclerenchyma fibre. Provided with such an arrangement any tension caused to sclerenchyma fibres causes the microfibrils to be pressed even more closely together. The cohesion of sclerenchymatous tissue is dependent upon the uninterrupted interlocking of the individual fibres. The sclerenchyma fibres, taken from a living plant, have been estimated to possess within the limits of their elasticity, a load-bearing capacity equivalent to the best variety of wrought iron or even steel The sclerenchyma fibres and their arrangement determine, to a large extent, the resistance to the bending of the stems and their columnar rigidity Their arrangement in the roots determines the resistance to stretching forces The sclerenchyma tissues are so arranged in an organ as to give it maximum firmness with minimum amount of sclerenchymatous tissue This is achieved by the absence of intercellular spaces between the sclerenchyma fibres, their arrangement in bands, strands, sheaths or shell-like layers.

In many monocotyledons, especially the xerophytic species, the vascular bundles near the periphery have extensive development of bast fibres outside the phloem, whereas towards the centre the amount of this mechanical tissue goes on decreasing and some inner bundles may be without them.

In many xerophytic leaves and stems, there are often cortical strands of bast-like fibres, especially just beneath the epidermis. In *Pycnanthemum virginianum* (mountain mint), the erect aerial stems possess columns of mechanical tissue at the stem angles in the cortical parenchyma. In *Torenia*, there are collenchymatous strands at the angles. It *Cucurbita*, there are collenchymatous strands below the ridges.

Rigidity and elasticity are the two main qualities that are essential for the plants to maintain their shape and form. Both rigidity and elasticity of plants, in general, depend upon the presence of collenchymatous and sclerenchymatous groups of cells. The position of these patches of thick-walled cells varies in various organs of plants. It mainly depends upon the influence of external forces upon the organs. The forces to which the plant organs are mainly subjected and the role of mechanical tissues are discussed in the following pages.

Influences of External Factors upon Mechanical Tissue.

Mechanical Stimuli. It is best explained by observations on the anatomy of tendrils. An unattached tendril has less tensile strength than the one that is attached, the latter sometimes being two to five times stronger than the former. Observations on a tendrillar climber, *Cyclanthera explodens*, have revealed that unattached tendrils remain thin and have less developed mechanical tissue as compared to the attached tendrils. The attached tendrils grow bigger in size (Haberlandt) and show greater development and greater thickening of the cell-walls in the chief mechanical strand. The vascular bundles

without a mechanical strand also develop them next to phloem. There is also an evidence that stems and other organs when subjected to tension develop extensive mechanical tissue. It has been claimed that growing stems of *Helleborus* subjected to tension develop best in regions where ordinarily none is present. The fruit stalks of *Cucurbita*, however, have more mechanical tissues when the fruits hang free in the air than when they rest on the ground. Roots react to mechanical stimuli more readily than do stems, tension resulting in a conspicuous increase in the number of mechanical elements and in the thickness of the walls, and compression resulting in a decreased cell size and an increased wall thickness.

If a young tree is fastened so that it can sway in but one plane, its diameter in this plane will be greater than in any other. Probably, the elliptical cross-section seen in trunks of sea coast trees is caused by wind, the long diameter being perpendicular to the coast line. In the spruce, the upper side of a horizontal branch is composed largely of white wood and the lower side of red wood. The former having about twice the tensile strength of the latter. The red wood whose elements have thicker walls possess the greater compression strength. The upper part of the branch is subjected to tension and the lower part to compression.

Desiccation. Observations on a number of plants have revealed that desiccation favours increased development of mechanical tissue. In dry air a mechanical cylinder is developed in the stem cortex of *Mentha aquatica*, while in moist air the cells remain parenchymatous. In the stem of *Ficus scandens* the cells that develop collenchyma in moist air become bast in dry air. In desert plants of irrigated soil, there is less mechanical tissue than in those that grow in dry soil. Aquatic and terrestrial stems of the same species *e.g*, *Polygonum amphibium*, differ widely in the amount of mechanical tissue developed ; the water form being too weak to stand alone, whereas the air form is very stiff. Observations on the anatomical features of hydrophytes, mesophytes, and xerophytes confirm this effect of desiccation.

The Role of Mechanical Tissues.

The Mechanical Features of Sclereids. The fact that ropes and cables are made from the bast fibres of hemp, ramie etc., indicates the tensile strength of [illegible]
chyma, as pith [illegible]
of the strongest ba [illegible]
of twelve to twenty-five kilograms per square millimetre, the higher figure being twice that of wrought iron. Bast fibres are considerably stronger when desiccated than when they contain moisture. They are no doubt more elastic under moist condit [illegible]
fication generally decreases tensile strengt [illegible]
of bast is due to the amount and quality [illegible]
dovetailing of the parenchymatous cells and, probably, also, to the spiral arrangement of wall micellae. Collenchyma is almost as strong as bast, though it has a lower limit of elastic elongation. Having the power of growth elongation, it is especially suited to growing tissues.

External to the bast is a collenchymatous cylinder and internal to the bast is the cylinder of secondary wood, which is of great mechanical importance. In angled stems such a *Pycnanthemum* (Fig. 16.6) and *Torenia*, strains are accentuated at the angles, where there is considerable collenchyma just inside the epidermis and often a patch of bast just outside the vascular tissue.

The advantage of flexile strength is well illustrated on mountain slopes that are subject to snow-slides and avalanches. Flexible trees and shrubs are uninjured, whereas some rigid trees (conifers) snap off like pipestems.

Compression Strength. The trunks of trees are subject to compression, owing to the weight of the parts above. Longitudinal pressure of this sort requires columnar strength. In many trees (as in walnut, red cedar, and most conifers), there is a solid supporting column whose central portions are the hardest and strongest. In some instances as in sycamore, the supporting column may become a hollow cylinder owing to the decay of the heart wood.

Roots and rhizomes are subject to radial pressure as they grow in diameter. A peripheral mechanical cylinder is the most effective means of resisting such radial pressure, and this is present in many rhizomes in addition to central mechanical strand. Prop roots are subject to unusual strains, since stem flexion causes severe tension on one side of the plant and equally severe compression on the other. The prop roots of corn often contain both central strands and peripheral cylinder of mechanical tissue, so that they are well-fitted to withstand strains of every sort.

Arrangement of Mechanical Tissues in Herbaceous Stems. In the herbaceous stems that are generally prone to flexion, the mechanical tissues are arranged in the peripheral portions. The arrangement of mechanical tissues in the sunflower stem serves as the best example. In this case, the peripheral and subepidermal cylinders of collenchyma, whose cell walls are highly plastic, resist compression. In addition, the patches of sclerenchymatous pericycle on the outside of vascular bundles (also called hard bast) bear the tension caused due to flexion of the stem. [illegible] ba[illegible] I-[illegible] the web of the grider whereas the flanges are formed by the opposite patches of hard bast. An individual girder of this type (Fig. 16.2) can resist the bending tension in one direction. But in stems like sunflower, there are many girders that form a ring around the vascular tissue

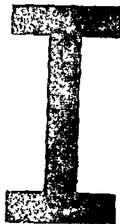


Fig. 16.2. An I-girder showing upper and the lower flanges with intervening web.

because they are bilateral organs. They are also prone to tearing and cutting effects by high winds. They bear the effect of transverse pressure by achieving stiffness due to cutinised outer wall of epidermal cells, which, in some cases, is supplemented by thickening of the lateral walls as in *Ficus* species, *Agave americana*, etc. Stiffness is also added by

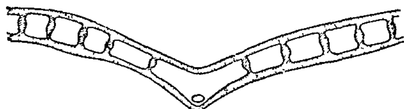


Fig. 16.4. Diagrammatic V.S. leaf of *Pandanus* showing I-beams of sclerenchyma between the two epidermal layers.

the presence of thick-walled hypodermis as in *Pinus* and *Nerium*. In the leaves of xerophytic grasses like *Ammophyla arenaria, Hemp, Pandanus* (Fig. 16.4) etc , patches of thick-walled bast fibres and other mechanical cells occur in-between the two epidermises and festoons of such cells often surround the vascular bundles. They form I-shaped beams and

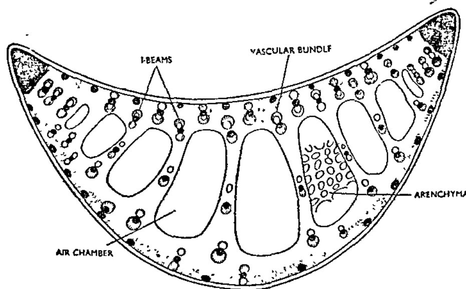


Fig. 16.5. T.S. (Diagrammatic) leaf of *Typha*. Note the marginal patches of sclerenchyma.

great amount of strength to the leaves as in *Banksia, Dasylerion*, *Pancratium* leaf, patches of collenchyma occur next to the

(Fig. 16.3) and can, therefore, resist the bending tension on all the sides of the stem *i.e.*, in any direction. The thin-walled cells of the pericycle, which flank the sclerenchymatous strands of pericycle (hard bast), act as shock absorbers and prevent the breaking of the girders under pressure In the stems of *Calatropis*, *Ranunculus*, *Vinca*, *Nerium*, etc., where sclerenchymatous pericycle is absent, this function is performed by the phloem fibres. In some cases *e.g.*, *Cucurbita* and *Dianthus caryophyllus*, there is an uninterrupted ring of sclerenchymatous pericycle out-

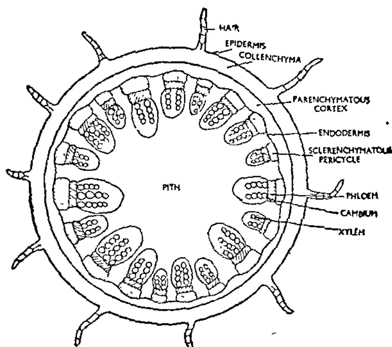


Fig. 16.3. Diagrammatic T.S. sunflower stem showing patches of sclerenchymatic pericycle. The opposite patches form an I-girder and the thin-walled patches of pericycle act as shock absorbers.

side the vascular tissue. Presence of two concentric rings of mechanical tissue in the peripheral portions of majority of herbaceous stems (outer ring of collenchyma and inner ring of sclerenchyma) enables them to resist both bending and compression caused by the flexion of the stem.

Arrangement of Mechanical Tissue in Woody Trees. For an account of this see under the heading 'Compression Strength' in this chapter.

Arrangement of Mechanical Tissues in Roots and Rhizomes. (See under the heading Tensile Strength and Compression Strength).

Arrangement of Mechanical Tissue in Leaves. The leaves are generally prone to transverse flexion at right angles to their surface :

because they are bilateral organs. They are also prone to tearing and cutting effects by high winds. They bear the effect of transverse pressure by achieving stiffness due to cutinised outer wall of epidermal cells, which, in some cases, is supplemented by thickening of the lateral walls as in *Ficus* species, *Agave americana*, etc. Stiffness is also added by

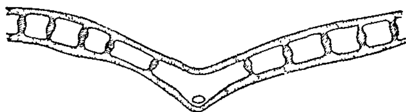


Fig. 16.4. Diagrammatic V.S. leaf of *Pandanus* showing I-beams of sclerenchyma between the two epidermal layers.

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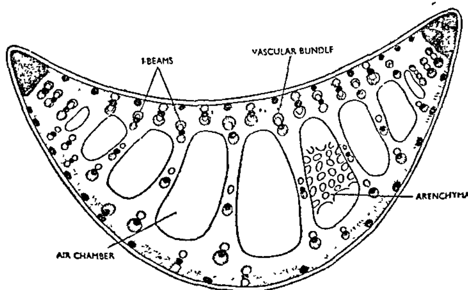


Fig. 16.5. T.S. (Diagrammatic) leaf of *Typha*. Note the marginal patches of sclerenchyma.

give great amount of strength to the leaves as in *Banksia*, *Dasylerion*, etc. In *Pancralium* leaf, patches of collenchyma occur next to the

layers of epidermis. In *Musa scpientum* and *Phoenix sylvestris*, patches of sclerenchyma occur next to the epidermal layer. Sometimes, as in *Osmanthus* (Fig. 5 4 A), evergreen leaves contain isolated mechanical cells (sclereids) extending from the lower to the upper epidermis, apparently acting as supports or braces Occasionally, these cells are either T-shaped or Y-shaped. In *Rhizophora*, the shape of the sclereids is H-shaped and is found in palisade cells. In the leaves of *Typha* (Fig. 16.5), *Eucalyptus* and *Pancratium*, the margins of the leaves possess patches of sclerenchymatous or collenchymatous cells. They save the margins of the leaves from the tearing effects of winds. Sometimes, the marginal protecting structures are wanting, as in the banana leaf, which consequently is shredded by the winds. Lobed leaves would seem especially subject to tearing at their sinuses ; in some cases, as in *Ribes aureum* strong arcuate veins just beneath the sinus prevent such tearing.

Arrangement of Mechanical Tissue in Petioles. The petioles of the leaves have to bear the weight of the leaf lamina and in order to remain erect and resist bending, the mechanical tissue is arranged in the peripheral parts. There are generally present strands of collenchyma and sclerenchyma below the epidermis or external to the

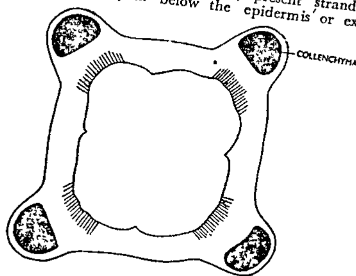


Fig. 16.6. Diagrammatic cross-section of square stem of *Pycnanthemum virginianum* showing mechanical tissue at the corners of the stem.

vascular tissue. In *Colocasia*, strands of sclerenchyma are present external to the vascular bundles. In *Eriobotrya japonica* and *Mangifera indica*, patches of sclerenchyma occur external to the vascular region.

Square Stems. In stems with squarish outlines, the mechanical tissue is found at the angles of the stem (Fig. 16.6) e.g., *Pycnanthemum virgiginianum, Capsicum annum, Torenia*. In *Tagetus, Peristrophe, Cucurbita*

etc., patches of collenchyma occur beneath the ridges, below the

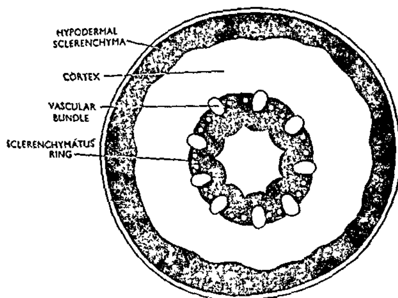


Fig. 16.7. T.S. (Diagrammatic) prop root of maize showing external and internal rings of sclerenchyma.

epidermal layer. These strands of mechanical tissue positioned at the angles afford sufficient strength to the stems so as to resist bending.

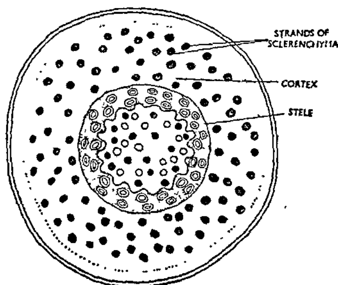


Fig. 16.8. T.S. (Diagrammatic) stilt root of *Pandanus* showing evenly distributed strands of sclerenchyma in cortex and pith.

In *Juncus balticus littoralis*, the outline of the stem is circular and it possesses alternating outer and inner fibro-vascular bundles in which a

bast cylinder completely surrounds each vascular bundle. The bast is more strongly developed outside than inwards. In another species of *Juncus*, the vascular bundles alternate with air spaces and the sclerenchyma (hard bast) forms I-beams towards the outer side of the vascular bundles. It is less developed towards the inner side.

(For distribution of mechanical tissue in Monocot stem see the first paragraph in the beginning of this chapter)

Distribution of Mechanical Tissue in Prop Roots and Stilt Roots. Prop roots (Maize) and stilt roots (*Pandanus*) are subject to unusual strains, since stem flexion causes severe tension on one side of the plant and equally severe compression on the other. The prop roots in maize contain both central strands and peripheral cylinders of mechanical tissue (Fig. 16.7) so that they are well-fitted to bear strains of every sort.

In the stilt roots of Pandanus (Fig. 16.8), there are evenly distributed strands of sclerenchyma in the cortex. The vascular bundles are also surrounded by a sheath of sclerenchyma. In pith also the sclerenchyma strands are evenly distributed. This type of arrangement of the mechanical tissue enables the roots to resist any type of bending and pulling strains.

17

ECOLOGICAL ANATOMY

In the preceding chapters, much stress has been laid on the anatomical features of the plants that usually grow under normal environmental conditions where they get adequate amount of water, optimum temperature and normal type of soil. Here and there some abnormal features and deviations from normal structure have been pointed out, but such deviations are concerning individuals having certain relations to their physical surrounding or to each other. The plants growing under normal environmental conditions are called **mesophytes** and the environments as **mesophytic.**

In the present chapter, we will deal with the anatomical features of the plants growing under abnormal conditions These abnormal conditions include excessive amount of water, scarcity of water, low and high temperatures, poor soils (such a sandy soil, gravel etc), plants growing as epiphytes, as parasites and those plants in which structural peculiarities are brought about by the attack of other parasitic plants such as fungi, bacteria and viruses The plants growing in water as free floating individuals or submerged under water at various depths or in mud are termed as **hydrophytes.** Such conditions are said to be **hydrophytic.** The plants that grow at places where water is scarce where, there is excessive transpiration, high temperature and poor soil are called **Xerophytes** and such environments are called **Xeric.** Plants growing in alkaline or salty soils or marshes are called **halophytes.** They also show xerophytic characters Epiphytes grow on other plants but have no organic connection with them The parasitic seed plants grow on their host with which they have established organic connection and draw upon their food and water *e.g., Cuscuta* Such plants show great structural variation in order to live under varied and abnormal conditions of the environment.

HYDROPHYTES

They can further be classified as : (*i*) submerged hydrophytes, (*ii*) floating hydrophytes, and (*iii*) amphibious plants.

Submerged Hydrophytes. They grow completely submerged below the surface of water, and show many note worthy structural peculiarities :—

Root

1. Their root systems are commonly reduced, both in length and in amount of branching.

2. Root hair may be absent.

3. The cuticle is either absent or poorly developed on the epidermal cells. This characteristic permits the water roots to absorb water and salt dissolved in it directly from the surrounding water.

4. *The cortex is wide* and possesses air-spaces (Fig. 17.3).

Williams and Barber (1961) suggested that the lacunar or air-space systems besides increasing organ's buoyancy and reinforcing its strength *through* inflation with gases, also offer resistance to bending stresses. The lacunate system is of great mechanical significance to the organs.

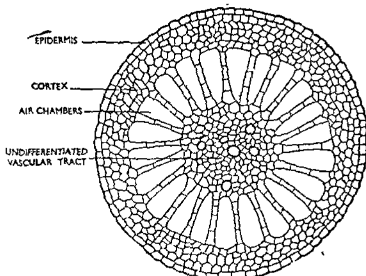


Fig. 17.1. [illegible] showing [illegible] cortex. [illegible]

5. The vascular tissues are poorly developed and have thin-walls (Fig. 17.3). Sometimes, the centre of the vascular tract is occupied by xylem cavity (Fig. 17.3). Vessels are absent in *Potamogeton* and many other hydrophytes.

Stem

6. The stem, in subm [illegible] it is prostrate. In some [illegible] The mucilage harbours [illegible]

7. The epidermis in the stem of hydrophytes is always single-layered and the cuticle is poorly developed. *In some cases, it may be* absent and only cellulose cell walls are present. This facilitates direct absorption of gases and mineral salts dissolved in water.

Although the [illegible] sumably allow [illegible] evidence that all [illegible] salts. Mayr (1915) observed that in strictly submerged species of *Ceratophyllum*, *Potamogeton*, *Myriophyllum* and *Sagittaria* and other genera, only certain groups of epidermal cells, stainable *in vivo* with various dyes, were easily permeable to salts. These localised groups of [illegible]

8. Hypodermis is absent. There are no collenchymatous or sclerenchymatous sub-epidermal layers.

9. The cortex is wide and extensively traversed by air spaces *e.g.*, *Hydrilla*, *Hippuris*, *Potamogeton*, *Myriophyllum*, etc. In *Myriophyllum* (Fig. 17.1), the air chambers in the cortex are symmetrically arranged. In *Hydrilla*, *Hippuris*, etc., there is no regularity in the arrangement of the air-chambers (Figs. 17.8 and 17.9). The lacunae are totally lacking in submerged members of the angiosperm family *Podostemaceae*. It is really an interesting case.

10. The cells in the cortex contain chloroplasts and its extensive development increases photosynthesis. The cell sap has low osmotic pressure.

11. The endodermis and pericycle layers are absent. The innermost layers of the cortex can, however, be regarded as endodermoid. These layers are quite distinct in the stem of *Potamogeton natans* (Fig. 17.10). In this case the pericycle is sclerenchymatous (Fig. 17.10).

12. The conducting elements are central in position and are not surrounded by any protective sheath or sheaths.

13. The phloem generally lacks phloem fibres.

14. The xylem elements possess thin walls and in some cases *e.g.*, *Potamogeton* (Fig. 17.11), *Hydrilla* (Fig. 17.9), the xylem is represented by a single large cavity in the centre. In *Elodea canadensis* (Fig. 5.7), and other hydrophytes, the vascular tract is undifferentiated. Xylem lacks vessels in *Potamogeton* stem. The corky layers are absent or rarely feebly developed in submerged organs.

Leaves

15. The leaves in the submerged hydrophytes are small and reduced *e.g.*, *Hydrilla*. In *Potamogeton* and *Vallisnaria*, the leaves are long and ribbon-shaped. In *Ceratophyllum* the leaves are segmented.

16. The leaf epidermis (Fig. 17.1 *b*, A—C) either lacks (*Potamogeton*) uticle or it is feebly developed, thus permitting easy absorption of salts dissolved in water, and gaseous exchange. The epidermal cells in *Ceratophyllum*, *Potamogeton* (Fig. 17.1 *b*) and *Myriophyllum* possess abundant chloroplasts.

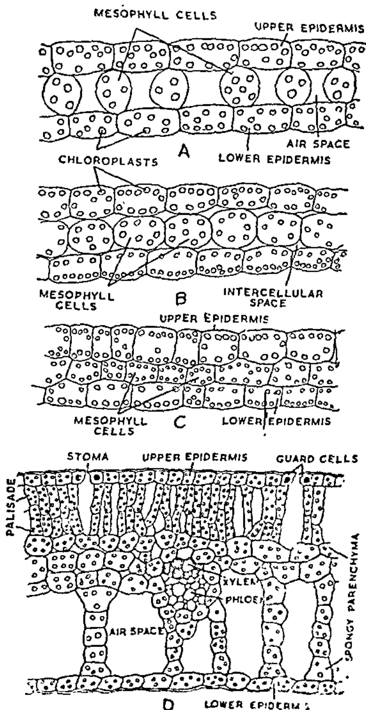


Fig. 17.1 b (A—D). Vertical sections through submerged and floating leaves of *Potamogeton*. A. V.S submerged leaf of *P. nodosus*. B. V.S. submerged leaf of *P. pusillus* C. V.S. submerged leaf of *P. natans*. D. V.S. floating leaf of *P. natans*.

17. There are no stomata in the epidermal layer of the leaves of submerged water plants (Fig. 17.1 *b*, A—C), If at all present, they are nonfunctional.

18. The mesophyll is undifferentiated and possesses well-developed air spaces *e.g.*, *Pontederia cordata*, *Potamogeton*, *Decodon.* In *Pontederia*, the partitions between the air chambers are also perforated. The cells contain abundant chloroplasts.

19. The vascular tracts are simple and sometimes very much reduced (Fig. 17.2). The xylem elements are thin-walled. Phloem is well-developed.

20. In *Potamogeton*, the submerged leaves are very thin and possess only a single layer of mesophyll cells (Fig. 17.1 *b*, A—C) between the two epidermal layers. In the floating leaves in *P. natans* (Fig. 17.1 *b*,D), there is well differentiated mesophyll.

The common submerged hydrophytes are . *Vallisnaria*, *Ceratophyllum*, *Potamogeton*, *Hydrilla*, *Elodea*, *Naias*, *Ottellia*, etc.

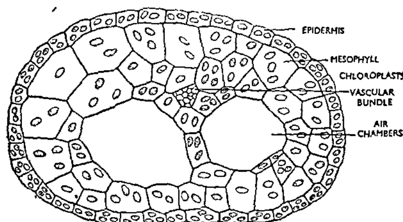


Fig. 17.2 *a*. Transverse section of a leaf segment of *Ceratophyllum demersum* showing an extremely simple conductive bundle. Note undifferentiated mesophyll with chloroplasts scattered in the cells. The epidermis also contains chloroplasts.

Floating Hydrophytes. Under this are included those hydrophytes (*i*) which have their leaves floating at the surface of water and their rhizomes rooted in the mud *e.g.*, *Nymphaea*, *Limnanthemum*, *Victoria rigia*, *Euryale ferox*, *Nelumbium speciosum* ; (*ii*) which are free-floating and are not fixed to the bottom of the pond *e.g.*, *Wolffa*, *Hydrocharis*, *Lemna*, *Utricularia*, *Neptunia*, *Trapa bisponia*, *Pistia*, *Eichhornia*. They possess the following characteristics :—

Roots

1. The roots are poorly developed. In *Lemna*, *Wolffia*, *Pistia*, *Eichhornia* etc., the roots do not possess root caps but instead have root pockets. In *Utricularia*, the roots are absent.

2. The root hair are also absent or poorly developed. The roots are not much branched.

3. The epidermis lacks cuticle or it forms a thin layer and this feature helps direct absorption of water and minerals dissolved in it from the surrounding water.

4. Cortex is extensively developed and possesses air spaces or even aerenchyma (Figs. 17.6 and 17.6 *a*).

5. The mechanical tissue is feebly developed or even absent.

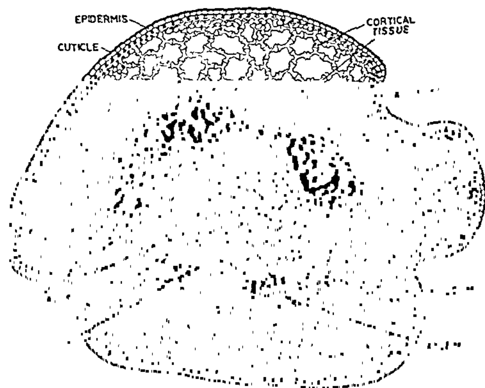


Fig. 17.2 *b*. T.S. Young Stem of *Polygonum barbatum*. Note the extensive air spaces in the cortex. The pith also has intercellular spaces.

6. The stele is centrally located and undifferentiated and the xylem vessels possess thin walls. In *Nymphaea* the xylem is well-developed but lacks vessels and consists of only *tracheids* and parenchyma (Fig. 17.6 *a*). In *Eichhornia* (Fig. 17.6) too the roots have well-developed xylem.

7. Cambium is not formed in the roots.

8. In the roots of *Lemna* there is no conducting tissue at all.

Stems

1. The rhizomes in *Nymphaea* and *Nelumbium* have well-developed

epidermis with copious secretion of mucilage. Hypodermis is also present.

2. The vascular bundles in *Nymphaea* are scattered in the cortex. The cortex possesses a large number of air spaces. Stellate sclereids are also found associated with the air spaces. The vascular bundles have thin-walled xylem elements.

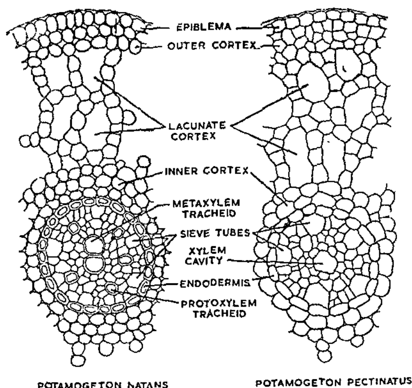


Fig. 17.3. Transverse section through roots of two species of *Potamogeton*. Note the difference in xylem.

3. There is no cambium between the xylem and phloem.

4. The phloem possesses a few narrow sieve tubes.

Leaves

1. The leaves lack or have thin cuticle over the epidermis. This increases the absorptive capacity of the leaf surface. In some cases, there is coating of wax on the upper surface of leaf (*Nelumbium*). The margins of leaves in *Victoria regia* are turned upwards.

2. The epidermis possesses chloroplasts in its cells *e.g., Utricularia.* ... ating leaves (Fig. 17.1 ... ja, 1968), stomata are found on the lower surface of the leaves during aerial

2. The root hair are also absent or poorly developed. The roots are not much branched.

3. The epidermis lacks cuticle or it forms a thin layer and this feature helps direct absorption of water and minerals dissolved in it from the surrounding water.

4. Cortex is extensively developed and possesses air spaces or even aerenchyma (Figs. 17.6 and 17 6 *a*).

5. The mechanical tissue is feebly developed or even absent.



Fig. 17.2 *b*. T.S. Young Stem of *Polygonum barbatum*. Note the extensive air spaces in the cortex. The pith also has intercellular spaces.

6. The stele ... xylem vessels po... loped but lacks ... (Fig. 17.6 *a*). ... oped xylem.

7. Cambium is not formed in the roots.

8. In the roots of *Lemna* there is no condu...

Stems

1. The rhizomes in *Nymphaea* and *Nel*...

Sagittaria, Alisma, Limnophylla heterophylla, Cardenthera triflora, Myriophyllum heterophyllum, Castalia, Typha, Proserpinaca palustris, Radicula

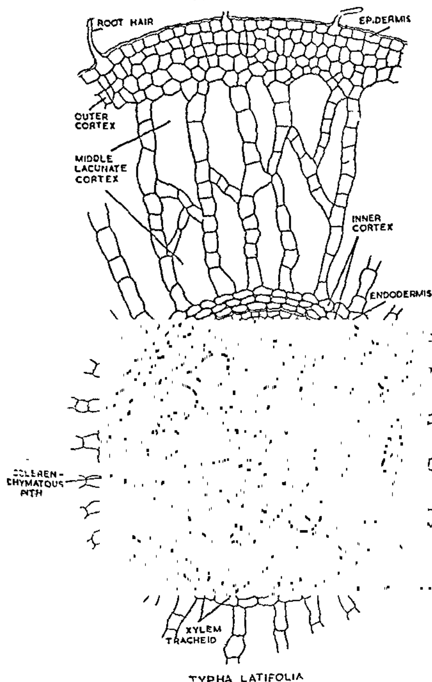


Fig. 17.5. T.S roots of *Typha latifolia*. Note the sclerenchymatous pith and conjunctive tissue.

aquatica, Sium acutaefolium etc. They show the following anatomical features :—

growth. They, however, become *obliterated* by *readjustment* of neighbouring epidermal cells. During initial stages of degeneration the guard cells show irregular thickenings on walls, disintegrated nuclei and highly vaculated cytoplasm.

3 The mesophyll is undifferentiated and traversed by air spaces. Its cells contain chloroplasts. In the leavrs of *Nymphaea, Victoria regia* and *Trapa*, the leaves have a well-developed palisade layer, sometimes even two layerd. In *Trapa* the mesophyll cells contain sphaeraphides. In *Nymphaea*, branched sclereids occur in the partitions of walls of air chambers.

4 The vascular tract is reduced and it is difficult to differentiate between xylem and phloem. Phloem in the leaves is comparatively well developed.

5. In water hyacinth (*Eichhornia*), the leaves possess swollen petioles with lots of aerenchyma.

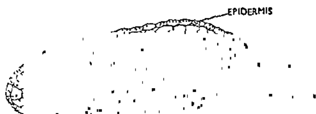


Fig. 17.4. T S. through the leaf of *Zanichellia palustris*.

In the partly submerged hydrophytes like *Ranunculus aquatilis*, species of *Trapa*, the leaves are heterophyllous. Those that are submerged are finely dissected and those that are above the surface of water have undissected lamina. The aerial leaves show well-developed cuticle on the leaves and stomata occur on upper surfaces.

Amphibious Plants. No plants show greater variations in leaf form and structure than do amphibious plants, which may be subject [illegible] *Ranunculus aquatilis*, [illegible] rial leaves which [illegible] much dissected. [illegible] with downward directed two lobes giving it the shape of an arrow. In deeper water the leaves show reduction in basal lobes which are absent in plants growing in very deep waters. Submerged plants bear thin leaves. All these stages can be found in a single individual, at different developmental stages. The plants of this species growing in mud show broad and distinctly sagittate leaves. Another group of amphibious plants, represented by *Alisma*, *Castalia*, and *Potamogeton natans* have narrow, submerged leaves, and broad thick aerial or floating leaves. The common amphibious plants are ; *Ranunculus aquatilis* (Fig. 17.7),

Sagittaria, Alisma, Limnophylla heterophylla, Cardenthera triflora, Myriophyllum heterophyllum, Castalia, Typha, Proserpinaca palustris, Radicula

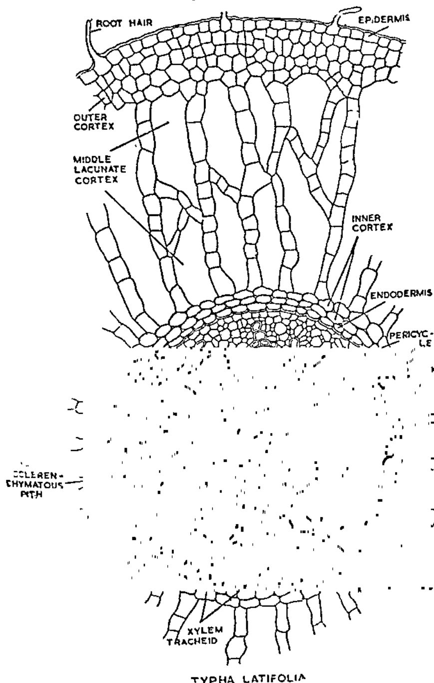


Fig. 17.5. T.S. roots of *Typha latifolia*. Note the sclerenchymatous pith and conjunctive tissue.

aquatica, Sium aculaefolium etc. They show the following anatomical features :—

Roots. 1. The roots are well-developed when they grow in mud and have distinct root caps. The epidermal cells have cuticle.

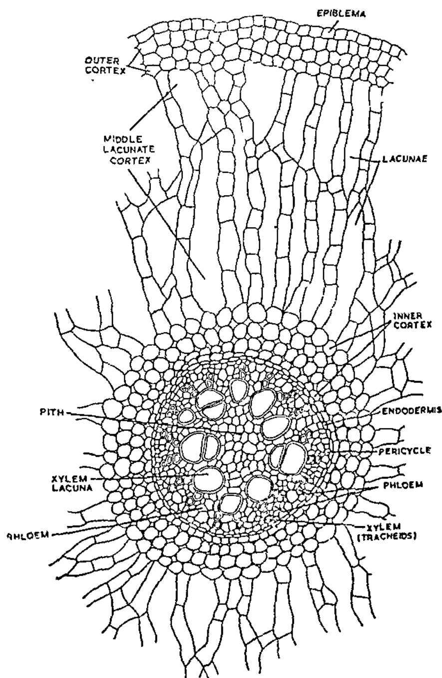


Fig. 17.6. T.S. Root of *Eichhornia crassipes.* The pith is parenchymatous.

2. The cortex possesses air-spaces.

3. The root hair are distinct.

4. The cortex has distinct and well-developed air spaces (Figs. 17.5, 17.6).

5. Distinct endodermis and pericycle are present Figs. 17.5, 17.6).

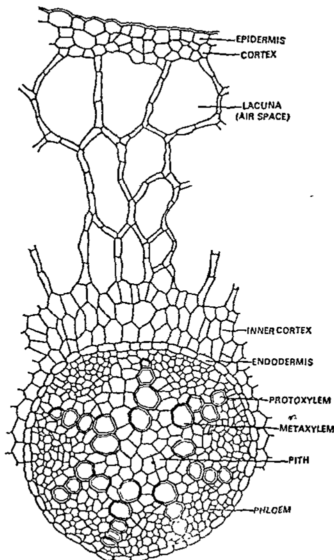


Fig. 17 6 *a*. Root of *Nymphaea*. The xylem lacks vessels and has only tracheids.

6. The vascular tissue is distinct and well developed in mud plants (Figs. 17.5, 17.6). It may be poorly developed when they grow in water.

7. In *Typha*, the roots have sclerenchymatous pith (Fig. 17.5).

Stem. 1. The epidermis shows a cuticle which is well developed in the rhizome of *Typha*.

2. The cortex in *R. aquatilis* (Fig. 17.7) shows aerenchyma and lacks any mechanical tissue In *Typha* the cortex possesses sclerenchymatous strands.

3. The vascular tissue is well-developed. Xylem is distinct from phloem and possesses thick-walled tracheids. Vessels are also distinct

Leaf. There are great variations in the internal structure of the leaf :—

1 The leaf epidermis in submerged leaves is poorly developed and lacks stomata In the exposed and aerial leaves epidermis possesses cuticle. The stomata are present in aerial leaves of other amphibians developed in *Typha* (Fig. 15.31).

2. In *Typha*, there are sclerenchymatous patches at the angles (Fig. 15.36) Such a sclerenchyma is absent in leaves of other amphibians such as [illegible]

3. [illegible]

In *Typh*[illegible]

by diap[illegible] Each air-space is lined with stellate parenchymatous cells. The diaphragms are traversed by vertical strands of sclerenchyma. Vascular bundles are also present in these thin-walled partitions In heterophyllous amphibians such as *Ranunculus aquatilis, Proserpinaca palustris* etc., the submerged leaves lack any differentiation in mesophyll. Their aerial leaves show differentiation into palisade and spongy tissues.

4. The vascular region is well-differentiated in the aerial leaves of heterophyllous amphibians In *Typha*, the vascular bundles are well-developed and show distinct xylem vessels. The phloem is also well-developed.

Typha is an example of a typical plant suited both for life in water as well as on land. Its anatomy clearly shows that it mingles both xerophytic and hydrophytic characters. Same is the case with *Equisetum*.

DESCRIPTION OF SOME COMMON HYDROPHYTES

Stem of Ranunculus aquatilis (Ranunculaceae, Dicot). A transverse section through the stem of *Ranunculus* reveals the following structures (Fig. 17.7) .—

Epidermis. It is made up of a single layer of thin-walled cells. There are no intercellular speaces between them. A thin cuticle is also present.

Cortex. It is parenchymatous and is traversed by numerous air-spaces. This is a hydrophytic character.

Endodermis. It is not clearly distinguishable as the cells lack casparian strips. The last layer of cortex can be regarded as endodermis. Esau uses the term endodermoid layer for endodermis, if it lacks casparian strips.

Pericycle is also indistinguishable.

Vascular Bundles. They are arranged in a ring and are discrete with wide medullary rays. Each bundle is capped by a patch of sclerenchymatous cells. These are the phloem fibres that become thick-walled and distinct. The bundles are conjoint, collateral, open and endarch.

Pith. It is composed of spherical and thin-walled cells with intercellular spaces between them.

Presence of air-spaces in the cortex is the hydrophytic characteristic. Other distinguishing features of the stem are : indistinct pericycle and endodermis, and phloem fibres forming sclerenchymatous sheath capping the vascular bundles.

In *Enhydra fluctuans* (compositae), the aquatic stem has no pith in the centre (hollow) in the internode. Below the epidermis is a continuous band of two-layered parenchymatous hypodermis. Next to it are the air-chambers. The endodermal cells contain starch grains. Bundles are capped with sclerenchyma patches which are phloem fibres. This stem differs from other compositae in possessing no collenchyma as hypodermis and in the absence of a distinct pericycle.

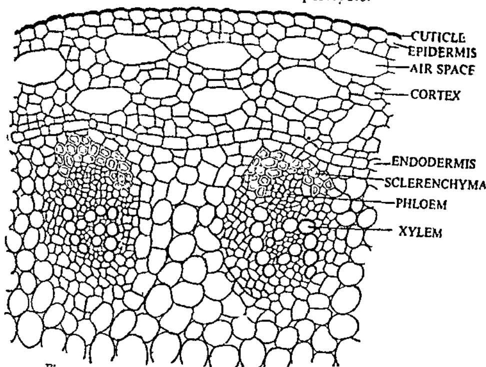


Fig. 17.7. T.S. through portion of a stem of *Ranunculus aquatilis*. Note the air spaces in the cortex and sclerenchyma patches forming a bundle cap. These are modified phloem elements.

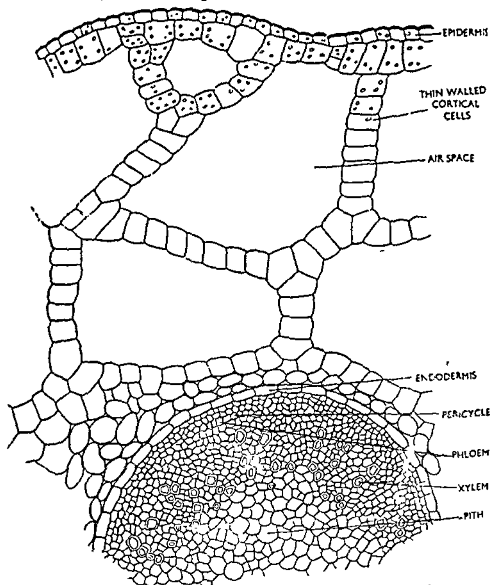
Stem of Hippuris. A transection through the stem of *Hippuris* shows the following arrangement of tissue (Fig. 17.8).

Epidermis. It is composed of a single layer of thin-walled cells, which may also contain chloroplasts. A thin cuticle is also present.

Cortex. It is traversed by big air-spaces (Fig. 17.8). The cells of the cortex are thin-walled and may contain chloroplasts. The partitions of the air chambers are made up of a single layer of cells. The air spaces have no regular arrangement. The sub-epidermal layer of cortex is composed of thin-walled cells without any air-space. The last layers of cortex have only intercellular spaces.

Endodermis. It is distinct and cells have no casparian strips. The pericycle is indistinct.

Vascular region. It consists of both phloem and xylem. The phloem forms the major portion of the stele and consists of sieve-tubes and companion cells. *It is restricted to the outer part of the stele next* to the endodermis and pericycle. There is no cambium. The xylem consists of scattered vessels and is not well-developed. The vessels have reticulate or spiral thickenings.



... stem showing large air-spaces in the ... The part labelled as pith is ... arenchyma.

Pith ... stem and consists of parenchymatous ... lular spaces. Solereder is of the

opinion that the pith is formed as a result of obliteration of the xylem elements and is known as **pseudopith.** Sanio (1865) observed thick-walled cells in the centre of the apex of the shoot. These thick-walled elements appear above the entry of the first leaf-traces, and farther from the apex become thin-walled and eventually disappear so that the centre of the stem in older plants is occupied by a homogenous 'pith-like' parenchyma. Arber (1920) fully confirmed Sanio's observations after examining serial microtome sections from the stem tip downwards. These observations suggest that pith-like central region in the stem of *Hippuris* is not true pith but xylem parenchyma and is designated as "**pseudopith**'. The stelar organisation in *Hippuris* stem is, therefore, protostelic (mixed protostele).

The hydrophytic features of this stem are :—(*i*) presence of air-spaces ; (*ii*) thin cuticle and absence of hypodermis ; (*iii*) absence of mechanical tissue ; (*iv*) The xylem is reduced.

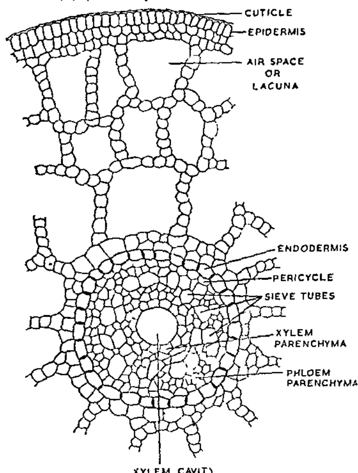


Fig. 17.9. T.S. stem of *Hydrilla* sp. Note the central xylem cavity surrounded by xylem parenchyma and phloem.

As a matter of fact presence of air spaces and absence of mechanical

tissue are the only hydrophytic characters. Poorly developed xylem is also encountred within many xerophytes.

Stem of Hydrilla. It is a common hydrophyte that grows submerged under the water. It has flexible stem which shows the following structure as revealed in a cross-section (Fig. 17.9).

Epidermis. It is made up of a single layer of radially elongated parenchymatous cells. The cuticle is feebly developed.

Cortex A few sub-epidermal layers are made up of loosely-arranged thin-walled cells with intercellular spaces (Fig. 17.9). Next to these layers the cortex is extensively traversed by large air-spaces separated by means of single-layered partitions. The last layers of the cortex are also without big air-spaces and possess only intercellular spaces.

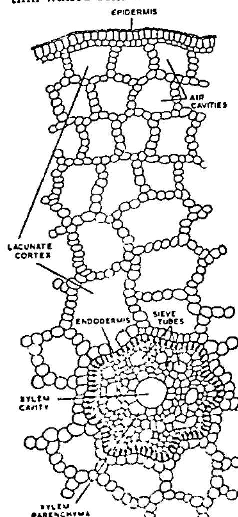


Fig. 17.10. T.S. stem of *Potamogeton pectinatus.* Note the abundant air cavities in the cortex. Xylem is represented by a single xylem cavity in the centre. Phloem is well developed and peripheral in position. The stelar organisation is protostelic as there is no pith in the centre.

The endodermis and pericycle are indistinct.

The vascular region consists of well-developed phloem with sieve-tubes and companion cells. Xylem is represented only by a single cavity in the centre. There is no pith. Xylem vessels are absent in *Hydrilla.* The vasculature in *Hydrilla* stem is also protostelic, because there is no pith in the centre.

Presence of air-spaces, feebly developed cuticle, absence of mechanical tissue, and extreme reduction of xylem are the hydrophytic characteristics of the stem.

Stem of Potamogeton. In this case there are either no subepidermal layers of loosely-arranged cells (Figs. 17.10 and 17.11) or a single layer may be present. The air-chambers are numerous and in some cases they directly abut against the epidermis. The endodermis is distinct and composed of radially elongated cells. The pericycle is indistinct. The xylem is represented by a single large xylem cavity in the centre in *P. P. pectinatus* (Fig. 17.10). In *P. natans* (Fig. 17.11), there are a number of xylem cavities. The vascular region, in this species, has well-developed fibrous layer next to the

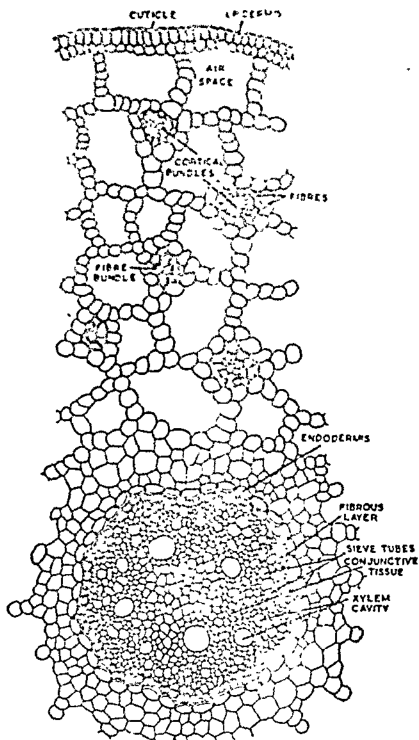


Fig. 17,11. T.S. through portion of stem of *Potamogeton natans*.

endodermis. Distinct pith is also present. There is a greater amount of variation in the arrangement and extent of vascular tissue in the various speices of *Potamogeton*. Fig. 17.12 gives a diagrammatic representation of the vascular region in the various species. There is no mechanical tissue. The xylem lacks vessels and has only tracheids. In *P. natans*, vascular bundles are also met with in the cortex (Fig. 17.11).

Various species of *Potamogeton* (Fig. 17.12) illustrate in a remarkable manner a gradual series in the fusion and reduction of the vascular bundles. In the stems of floating leaved species, such as *P. pulcher* and *P. natans*, the stele contains several groups of more or less distinct leaf traces (Fig. 17.12) and cauline bundles. The bundles are condensed into three groups in both *P. crispus* and *P. lucens*, but in the latter case, there is considerably more reduction of xylem and phloem regions (Fig. 17.12). In the linear leaved submerged species, such as *P. pusillus*, the xylem groups of all the individual bundles have become fused into

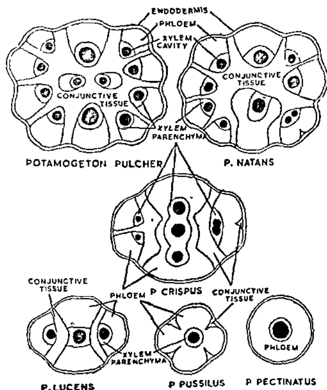


Fig. 17.12. Diagramatic cross-section of stems of various species of *Potamogeton* illustrating the fusion and reduction of the vascular tissue.

a single axial passage but areas of phloem remain separate, whilst in *P. pectinatus*, there is more or less homogenous zone of phloem surrounding the axial lacuna or space. Some species of *Potamogeton* (*e.g.*, *P. natans* : Fig. 17.10) also possess minute vascular strands running

Stem of Limnanthemum (*Fig. 17.13*). The epidermis is composed of a single layer of radially elongated cells with feebly developed cuticle. There are a few layers of sub-epidermal cortical cell that are *loosely-arranged (Fig. 17.13). The cortex consists of numerous air-sacs* bounded by single rows of thin-walled cells. The last layers of cortex are also composed of loosely-arranged thin-walled cells. The endodermis is distinct and its cells contain starch grains. The pericycle is indistinct. The stem has a main central stele that consists of scattered

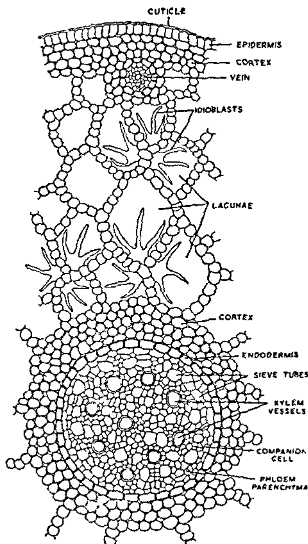


Fig. 17.13. T.S. stem of *Limnanthemum*. Note the [illegible] scattered [illegible]

[illegible] ...enchyma [illegible] absent. The other vascular bundles are small and scattered in cortex and consist of phloem with xylem represented by a single vessel (Fig. 17.13). The stelar organisation in this stem is a mixed protostele.

Stem of Myriophyllum :

In this case (Fig. 17.1), the air-spaces are symmetrically arranged and have thin partitions made up of a single layer of thin-walled cells. There is a distinct zone of thin-walled cortical cells next to the epidermis The endodermis and pericycle are absent. Vascular tissue is poorly developed. The xylem consists of a few scattered vessels surrounded by phloem. The stelar organisation is protostelic.

Leaf Segment of Ceratophyllum Demersum. A transverse section (Fig 17.2) through the leaf segment of *C. demersum* has an almost oval outline and reveals the following structures :—

Epidermis. It is made up of a single layer of thin-walled cells. Cells contain chloroplasts.

Mesophyll. The mesophyll is undifferentiated and consists of large thin-walled cells with a few large intercellular spaces. The cells contain scattered chloroplasts.

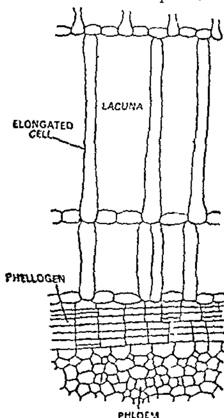


Fig. 17.14 V.S. portion of stem of *Justiaea peruviana* showing loose lacunar tissue or aerenchyma with elongated cells arranged in radial rows.

The vascular tissue is undifferentiated and poorly-developed. There is no distinction into xylem and phloem. It is represented by a small vascular tract containing a few thin-walled elements. There is no mechanical tissue and the stomata are also wanting.

Presence of air-spaces, absence of stomata, thin cuticle, undifferentiated mesophyll, absence of mechanical tissue, and poorly-developed vascular system are the hydrophytic characters of the leaf.

In the stem of *Jussiaea peruviana* (Fig. 17.14), phellogen in submerged stems gives rise to loose lacunar tissue or aerenchyma. The cells become elongated and arranged in radial rows. The stem in such conditions develops capacious air-spaces which give it a swollen appearance, and frequently the aerenchyma grows so rapidly as to break through the bark, forming whitish patches ; the so-called water lenticels are similar patches of whitish tissue formed under identical conditions.

The common occurrence of the spaces or the lacunar tissue in the water plants is attributed to the weak transpiration. They develop maximum at places where transpiration is low or almost absent. The

exact mechanism, whereby the reduction of transpiration influences tissues so as to produce large air-spaces, is for the present, not known.

HYGROPHYTES

Hygrophytes are those plants that live in perpetually damp habitats. These plants have to cope with the absorption of lot of water from the damp soil and then the movement of water through their body and then ultimately to pass it out into the very humid atmosphere. Such plants possess peculiarities of structures which promote excessive transpiration. Such a condition is called **hygromorphy.** Such plants cannot grow in dry habitats and, if the air becomes dry, they will also dry. They show the following characters :—

1. The leaf blades are thin, delicate and large. They have rich sap contents.

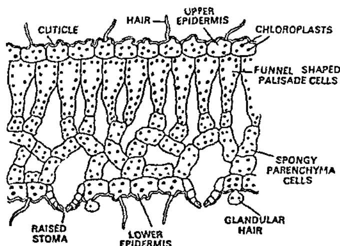


Fig. 17.15. T.S. leaf of *Ruellia portellae* (hygrophyte).

2. The leaves are glabrous and the epidermis is covered with *numerous hair or papillae thus giving a velvet-like appearance to the* lamina. This feature increases the transpiring surface.

3. The epidermal cells are large in size and contain chloroplasts. The large size of the cells is correlated to their water storage capacity which prevents the leaves from wilting during the drier periods of the year.

4. The cuticle is thin.

5. The stomata are raised above the epidermis (Fig. 17.15).

6. The mesophyll may or may not be distinguished into palisade parenchyma and spongy parenchyma. *Its cells are large and* enclose wide air-spaces (Fig. 17.15).

7. Many hygrophytes possess hydathodes.
8. The vascular systems are weakly-developed.

XEROPHYTES

In most respects the xerophytes are the reverse of hydrophytes in their structural features. The characteristic structures of xerophytic plants have long attracted the interest of ecologists and provide much of the subject-matter for the science of ecological anatomy. Where water is relatively scarce or the amount that can be absorbed is limited for other reasons (as in saline) or where evaporation is excessive, plants display characteristic structural features.

1. The roots are frequently strongly developed (though not in cacti) possessing either considerable length (*Calotropis, Welwitschia*) or greater size ; roots of the latter class accumulate large amounts of water and food. In some extreme xerophytes, the root hair extend to the root tips (*Opuntia*), and in certain cases they possess rigid, thickened walls (*Pinus edulis*). In some cases *e.g., Asparagus*, the roots become fleshy and store water. Such roots contain mucilage also.

2 The leaves in the xerophytes show far greater variation. In certain xerophytes (plants capable of growing more or less under dry conditions), the leaf tissues are closely packed and exceptionally thick layers of cuticle are produced (*Dianthus caryophyllus, Agave americana*). In some cases *e.g., Salix glaucophylla* a thick layer of wax grains is present outside the cuticle. In *Ficus elastica* and *Nerium*, there are three layers (Fig. 15.1) of epidermal cells. In the former case, the cells possess thick wall. The stomata are in pits (*Nerium*). The palisade tissue is well developed. In *Nerium* (Fig.15.1), *Atriplex, Ficus elastica*, the palisade layers are found next to the upper as well as the lower surfaces The spongy tissue is found between two palisade layers. In *Greggia camporum* and *Sphaeralcea incana*, the whole mesophyll is composed of palisade tissue In the latter case the epidermis is thickly covered with trichomes. Such leaves are called **trichophyllous**. In *Atriplex* the epidermis bears numerous vascicular hair. In many cases sclerenchymatous hypodermis is present (*Pinus*). It is thought to redue the injurious effect of wilting. Such leaves are called **sclerophyllous** leaves.

The foliage leaves of many xerophytic plants have thick fleshy leaves composed chiefly of water storage tissue ... sist of an epidermis, sev... a), but more commor ... y con- storage tissue is intern ... 17.16

In *Mesembryanthemum* ... called **Malacophyllous.** ... the water much distended and project considerably beyond the epidermal level, In *Mesembryanthemum crystalinum*, a few of the epidermal cells are causing the leaves to glisten in the sunlight.

In some cases as *Casuarina* and *Equisetum*, the leaves are reduced and scale-like. Such xerophytes are called **Microphyllous.**

3. Protective features are remarkably developed both in amount and in kind, and their advantage is undoubted, owing to the great exposure of xeorophytes to transpiration. Many species are leafless, the cylindrical stems exposing a relatively small surface to transpiration. In many cases there is a temporary reduction in surface, as in involute leaves of grasses, as in those legumes whose leaves close in dry weather as in **"resurrection plants"**.

4. In woody xerophytes, there is a prominent bark development, the cork in particular being of high significance in checking transpiration. The surfaces of both leaves and stems are covered with spines (*Solanum xanthocarpum, Argemone mexicana, Carthamus oxycanthus*).

5. Oil and resins are often abundantly developed (*Pinus*).

6. Presence of sap and latex (Many Euphorbias and Cacti).

7. The osmotic pressure of the cell sap is often high.

8. The conductive tracts are prominent, the vessels being larger and longer and the walls thicker than in moist plants. Lignification is prominent and annual rings are well-developed.

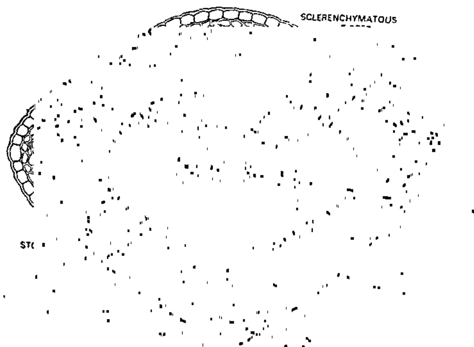


Fig. 17.16. T.S. needle of *Pinus roxburghii*

9. Bast fibres and other mechanical elements reach their highes development in the xerophytes.

10. Cells are smaller in size and thick-walled, especially in leaves.

11. *Xylem cells are smaller in size* (diameter).

12. The epidermal cells are less sinuous and possess more liquids on the transpiring surface (Clark and Levitte, 1956).

The characters described above are non-inherited structural characteristics that are produced as a *result of exposure to an unfavourable* water balance during tissue differentiation. Thody (1933, 1—6) referred to these characteristic as **xeroplastic.**

Besides the structural features described above, the xerophytic plant exhibit the following *physiological characteristics* :—

1. Rate of transpiration per unit area is *greater inspite of the* reduced net rate of transpiration (Maximov, 1929).

2. The rate of photosynthesis per unit area is rapid.

3. Levitt (1956) and Iljin, (1957) have shown that the ratio between starch and sugar is also lower in these plants.

4. Osmotic pressure is higher.

5. Iljin (1957) has found that protoplasm is *less viscous* and more permeable in the xerophytic plants.

6. They are *resistant to wilting.*

7. They flower and bear fruit earlier.

8. The percentage of **bound water** (that *fraction of* water which is absorbed by the colloids so strongly that it does not act as a liquid) per unit dry weight of tissue is greater (Whitman, 1941).

[illegible] they must either endure [illegible] nifold devices, [illegible] very little in common morphologically, physiologically [illegible] tomically, can be recognised. These are : (*i*) *Ephemeral annuals*, (*ii*) *Succulents, and* (*iii*) *Nonsucculent perennials.*

Ephemeral annuals.

The ephemeral annuals are small plants that grow in the arid regions of the world. These plants germinate and grow quickly during the short rainy *season and* reach maturity. They bear flowers and set seeds during this short period. These plants can bear the atmospheric drouth but not the soil drouth. They p[illegible] dry seas[illegible] ans of their [illegible]

and succulent leaves. Succulence in both the cases is due so proliferation of cells in parenchymatous regions, accompanied by reduction in the size of the intercellular spaces, and enlargement of the vacuoles.

Fleshy xerophytes. They possess succulent stems *e.g., Opuntia, Echinocactus, Cereus, Euphorbia royaleana.* etc Their anatomical characteristics are revealed if we study a transection of the stem. In Opuntia the stem is covered by an epidermal layer composed of thick-walled cells. The cuticle is also well-developed and forms a thick layer. Below the epidermis is a two to three-layered collenchymatous hypodermis. Next to this is the chlorenchymatous cortex. This region is made up of three or four layers of palisade-like cells which contain abundant chloroplasts and serve as photosynthetic region. Next to this region is the water storage tissue, which consists of large thin-walled cells with a few small intercellular spaces. The cells are highly vacuolate and contain mucilage that can hold water. The same type of arrangement of tissues is found in *Euphorb'a royaleana* and *Cereus.* Some of the cacti *e.g.*, the giant cacti (*Cereus giganteus*) are known for their water storage capacity. In *Cavanillesia,* the trunk assumes the shape of a barrel. During rainy season the stems accumulate large quantities of water, which becomes depleted during the subsequent drought. The fluted stems of *Cereus giganteus* undergo accorddon-like expansions and contractions during wet and dry periods respectively, the maximum circumferential difference being considerable. These plants have their leaves and stipules reduced to spines.

Succulent Leaves or Malacophyllous Xerophytes. Common examples of plants with succulent leaves are : *Begonia, Salsola kali-tenuifolia, Senecio, Bryophyllum, Kalanchoe. Agave, Aloe, Yucca, Gasteria, Haworthia, Mesembryanthemum, Peperomia, Sempervivum assimile, Tradescantia.* These plants possess a **water tissue** which consists of turgescent parenchyma cells with delicate cellulose walls, thin peripheral layers of cytoplasm, and few or no chloroplasts. In many succulents, the water tissue is not sharply delimited from ordinary chlorenchyma, and may be made up entirely of turgescent green cells, or the leaf may be thick with chlorophyll decreasing towards the centre (*Senecio*), the cells otherwise similar in all respects as in most crassulaceae ; or the leaf may be thick with chlorophyll decreasing towards the centre, but with the outermost chlorenchyma cells elongated, representing true parenchyma cells, while the cells in the centre become more and more isodiametric and also poorer in chlorophyll *e.g., Agave americana.*

In *Salsola Kali-tenuifolia* (Fig. 15.14), the leaves are succulent. A cross-section through such a leaf reveals an epidermal layer of parenchymatous cells with a thin cuticle. Next to the epidermis is the chlorenchymatous palisade tissue. It is followed by a large central water tissue which is composed of large, thin-walled cells with no intercellular spaces (Fig. 15.14). In this case,
located and is sharply delimited fror
the, water storage tissue is centrally

has a comparatively thick cuticle. Other leaves belonging to this category are *Hakea* : in which the peripheral portions of the cylindrical leaves are occupied by one or two layers of chlorenchyma with ostrosclereids scattered among them. The epidermis is thick-walled in *Yucca*, and *Agave*. *Sansevera*, also, belongs to this category.

A third kind of water tissue differs from all the rest in its peripheral position. In such cases, the epidermal cells store water. In *Peperomia* (Fig. 17.16,*a*), the epidermis is three or four layers thick. The outer layer is of small cells (*Fig.* 17.16,*a*) whereas the inner layers have larger cells with thin walls. They store water. Here and there, a few mucilage

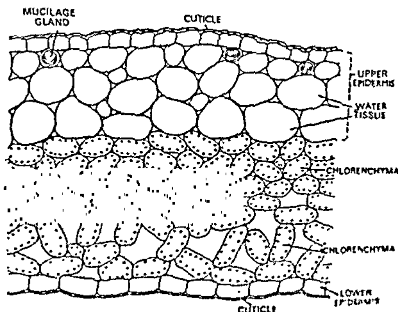


Fig. 17.16 *a*. T. S. through leaf of *Peperomia*, illustrating peripheral or epidermal water tissue, the epidermis being three or four layers thick. Also note the mucilage glands and centrally placed chlorenchyma.

glands are also present below the uppermost layer (Fig. 17.16,*a*) The centrally placed chlorenchymatous tissue consists of upper layers with small and closely packed *cells with* abundant chloroplast, while the lowermost chlorenchyma layers consist of larger and more loosely arranged cells with less chlorophyll. *In Tradescantia*, the peripheral *water mantle* is single or double-layered and consists of large turgescent colourless cells. In *Begonia* also the water mantle is peripheral and

In *Asparagus* and *Ceiba parvifolia,* the roots store water. The cells contain mucilage which absorbs and retains water.

Nonsucculent Perennials. This class of xerophytes includes all nonsucculent herbs, shrubs and trees that can endure wilting. This endurance is limited to a short period as in most woody plants, or may extend to months and even to years in grasses, sedges and some herbs. They are able to endure this wilting by way of numerous physiological, morphological and anatomical characteristics. There are no definite anatomic or physiologic characteristics common to all members of this class. They vary from species to species and each one of them has solved the water balance problem in its own peculiar combination of adaptive characters. Two plants growing side by side in a xeric atmosphere possess entirely different characteristics to adapt to a similar environment. Some of the principal characterstics shown by such plants are listed below :—

1. The root system is profusely developed and there is a rapid elongation of the tap roots. In *Prosopis* and *Alfalfa,* the roots grow to the depths of 19·50 m. and 38·70 m. respectively. The roots in *Calotropis procera* also grow very deep in the soil and make a permanent contact with the moist subsoil. In *Pinus edulis,* a true characteristic of desert borders, the roots possess rigid and thickened walls. Same is true in the case of *Calotropis.*

2, The plants possess high osmotic pressure which is a physiological development necessitated by high solute content of the unleached soils.
transpir.
laying
which might take place under extreme desiccation.

3. They can minimise the rate of transpiration during extreme conditions of desiccation that bring about wilting. This is accomplished in several ways that include, (*i*) dying back of leaves *e.g.,* many grasses. (*ii*) rolling of leaves *e.g*, *Ammophila arenaria* (Fig. 17.19), (*iii*) by producing special set of leaves during dry periods and (*iv*) by bearing delicate leaves during rainy season and then shedding them immediately when ground water is exhausted *e g., Euphorbia splendens.*

4. Those xerophytes which retain their leaves during dry periods show the following characteristics :

(*i*) Leaves are cutinised *e g., Pinus, Quercus sp., Dianthus.*

(*ii*) They possess waxy coating *e g. Salix glaucophylla.*

(*iii*) The stomata are smaller in size and remain closed.

(*iv*) Sunken stomata *e.g., Nerium* (Fig. 15.1). In *Nerium* the stomata are present in pits whose surface is lined with hair.

(*v*) Densely pubescent (trichophyllous) surfaces also minimise the rate of transpiration because they keep the air currents well-elevated

above the stomata *e.g.*, *Calotropis*, *Cercocarpus*, *Eleagnus* etc. In *Poa*, the epidermis undergoes characteristic folding during desiccation.

(ii) Folding of leaf surfaces as many legumes growing in deserts fold their leaves upwards and protect almost half the surface from

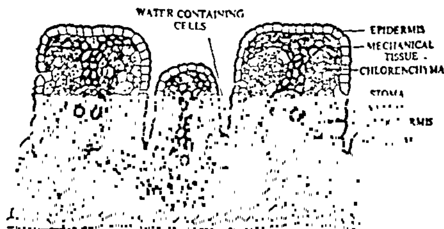


Fig. 17.17. Transsection of an involute leaf of *Ammophila arenaria* showing water containing cells in the sinuses, hypodermal sclerenchyma below the ridges and compact arrangement of chlorenchyma cells which are elongated.

desication. The leaves in *Ammophila* are thrown into ridges and grooves (Figs. 17.17, 17.18, 17.19). The epidermis is composed of a single layer of slightly thick-walled cells with a layer of cuticle. Certain cells of the epidermis situated in the sinuses are larger in size and turgid. These are water-containing cells and control the leaf-closing and leaf



(*vii*) Presence of many-layered epidermis is in *Nerium* (Fig 15.1) also *gives rigidity to the leaf and prevents shrinking.*

(*viii*) In sclerophyllous xerophytes *e.g.*; *Banksia* and grasses, the leaves possess a subepidermal sclerenchymatous layer which gives rigidity to the leaf and prevents shrinking.

5. **Microphyllous leaves.** In some xerophytes *e.g.*, *Casuarina*, the leaves are reduced in size and are scaly. It has been experimentally proved that reduction in the size of leaves does not reduce the rate of transpiration ; rather it increases the potential transpiration per unit area. This reduction in size has, no doubt, a fundamental role to play and it has been shown that it reduces the likelihood of necrosis, and the small size of the leaves also prevents the leaf surface from overheating when exposed to strong solar radiation. In such plants, the stems perform the functions normally attributed to the leaves. In *Casuarina*, the stem is ridged and grooved and there are sclerenchymatous patches below the ridges that are followed by a few layers of chlorenchymatous cells. The stomata are restricted to the lower halves of the furrows. In *Casuarina*, there are hair in the furrows. These hair contain water and keep the furrows cool.

Capparis aphylla, a common xerophyte in India, also belongs to this category. In this case, the leaves are scaly and usualy fall off immediately after the rainy season and the stem bears paired stipular spines. The stem has thickened epidermal cells that have lignified walls. The cortex possesses bone-shaped sclereids whose upper ends touch the epidermis. Thick-walled epidermis and the sclereids afford mechanical strength to the stem.

6. The cell size and the size of the vacuoles is reduced in the non-succulent xerophytes. The reduced cell-size in the plant organs possibly prevents the pulling away of the protoplasm from the cell-walls and rupture of plasmodesmata under conditions of drought and desiccation. Smaller size of cells in no way helps minimising the rate of transpiration.

Zalensky (1904) observed that veining of the leaves in the plants growing in dry, open spaces was much more abundant than in the leaves of those in the shade or in protected spots. The cell size was also smaller. These observations he then extended to a comparative study of the structure of leaves on the same tree. In *Dactylus glomerata*, Zalensky (1904) found that, as a rule, leaf structure changed with level of insertion on the tree, the structure being more xeromorphic with increasing distance from the root. The progressively higher leaves had smaller cells throughout, smaller stomata and more of them per unit-area, thicker and less sinuous walls in the epidermal cells, a greater contrast between the palisade and spongy layers, intercellular spaces and better developed mechanical tissue. Xeromorphy in these upper leaves seems unlikely to be an adaptation for reducing loss. Indeed, it has been shown that the upper leaves transpire

rapidly than lower ones. These results have cast doubt on the adaptive character of the traits of xerophytes in general. Maximov calls attention to the fact that when water is abundant many xerophytes transpire more rapidly than mesophytes and it is only under drought conditions that their water loss is markedly cut. He attributes this and, therefore, the quality of drought resistance in general, not to any structural traits but to protoplasmic character, notably osmotic concentration and changes in cell colloids that would enable the plant to conserve its water supply and thus endure dry condition better than other plants. Eckardt (1953) and Iljin (1957) agree with this conclusion. Shields (1950), who has reviewed the whole subject of xeromorphy, agrees in general with Zaenski, Maximov and Yapp that this type of structure (small size of cell etc.) has little significance as an adaptation in drought resistance. Many of the structural characteristics of the xerophytes, she suggested, may be the result of physiological differences. Thick cell-wall and abundance of mechanical tissue may result from active photosynthesis in plant where all its products cannot be used in growth because of the shortage of water.

Ashby (1948 b) attributes the small size of the cells in the upper leaves as due to the influence of immature leaves above them, an influence which may be hormonal in character.

Muller-Stoll (1947 b) has the evidence that xeromorphy of plants in peat bogs is due to a deficiency of nitrogen rather than of water.

Penfound (1931) as a result of experiments found that plants growing in moisture show a relative decreases in xeromorphy *but develop* increased amount of xylem.

Sun Leaves and Shade Leaves. Leaf structure is *often different* in different light intensities (Fig. 17.20, 17.21). The sun leaves have generally the following characteristics :—

1. Thick cuticle.
2. Epidermis thick-walled.
3. Palisade tissue well-developed and many-layered (Fig. 17.20).
4. Surface hairy.
5. Leaves have generally smaller laminar area.
6. Veining is more pronounced.
7. Margin generally serrated.
8. Petioles shorter.

The shade plants generally possess : (*i*) *thin cuticle.* (*ii*) epidermis thin-walled, (*iii*) palisade not well-developed and sometimes there is no

distinction into plaisade and spongy parenchyma, (*iv*) lamina well-developed and with longer petioles, (*v*) veining less prominent, (*vi*) surface not hairy

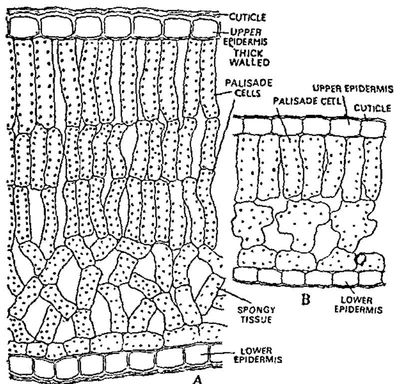


Fig. 17 20 A.T.S. through sun leaf of *Tilia* B.T.S. through shade leaf of *Tilia*.

EPIPHYTES

Epiphytes are those plants that grow upon other plants but do not derive any food and water from them. They do not have any connection with the soil. They possess aerial roots that are hygroscopic and obtain their water supply from the humid environments *e.g.*, *Dandrobium*. The **nest epiphytes** spread their roots over the surface of the plant in such a manner as to be well-situated to absorb water even in case of a small shower. The roots also accumulate large amount of debris that can hold water like the soil. In *Dandrobium*, the aerial roots that hang in air are thick, unbranched and whitish-green in colour. The surfaces of these roots are covered by several layers of special water-absorbing cells, called the **Velamen**. These cells are dead and empty. The water absorbed by them is later taken up by the living cells of the root. Next to the velamen is a layer of thick-walled suberised cells, called **exodermis**. Some cells in this layer are thin-walled and are known as passage cells. These cells permit the passage of water from velamen to the cortex.

The most remarkable instance of an epiphyte that absorbs water by means of leaves and stems is *Tillandsia usneoides* (Bromeliaceae). In this case roots are absent or feebly developed and serve only as anchorage organs The stem is repeatedly branched and bears small peltate scales that collect capillary water which is absorbed by small uncutinized spots on the epidermis.

In Pineapple, the upper epidermis in the leaves has wavy outline and numerous water absorbing peltate scales are present in the depressions. These absorb moisture from the environment.

Numerous other orchids like *Vanda*, *Cymbidium*, *Eria*, grow as epiphytes on forest trees in India. They have sometimes succulent stems and leaves. In some, there are succulent pseudobulbs. Thick cuticle, sunken stomata, reduced leaves, are also some of the characteristic features of the epiphytes. These epiphytes, which spend their entire life on the supporting plants, are called **holo-epiphytes**. Some common epiphytes that are found in India are : Orchids, such as *Dendrobium*, *Vanda*, *Eria*, etc , *Scindapsis officinalis*, *Pothos scandens*, (Araceae) ; *Dischidia rafflesiana*, *D. nummularia* (Asclepiadaceae) ; *Cereus triangularis* (Cactaceae). Many ferns like *Asplenium nidus*, *Pleopeltis*, *Polypodium fissum*, *Woodwardia canadensis*, *Cystopteris bulbifera*, *Cyclosporus adnascens*, *Drynaria quercifolia*, commonly occur as epiphytes. Numerous liverworts, lichens, algae, and fungi can be regarded as epiphytes.

PARASITES

Parasites are plants that derive food or food materials from other plants to which they are attached. A holoparasite is one that is entirely dependent for its food upon the organism to which it is attached *e.g.*, *Cuscuta*, *Orobanche*, *Conopholis*, *Lathraea*, *Epifagus*, *Rafflesia*, *Tozzia*, etc. A partial parasite is one that is only partially dependent upon the organism to which it is attached, being capable of manufacturing a part or even all of its food *e.g.*, *Viscum*, *Loranthus* *Arceuthobium*. They show some characteristic features. In *Cuscuta*, the stem is weak, yellow and bears only scale leaves. The chlorophyll is absent. The stem bears adventitious roots called the haustoria which penetrate the host and establish contact with its conducting elements. The haustoria absorb water and inorganic salts from the xylem and food materials from the phloem.

...and *Santal-* because ... prepare their own food because they ...

MYCORRHIZA

Fungi are associated habitually with the roots of many plants, such as oaks, pines, orchids, and cycads. This association between a

fungus and a root of a seed plant is called **Mycorrhiza.** In *Pinus* the mycorrhiza is **ectotrophic** because the fungal hyphae invest the root. In Pinus, there are long roots which bear root hair, and short and coralloid roots which are mycorrhizic and lack root hair. This mycorrhiza induces the root to branch repeatedly giving it a coralloid appearance. The hyphae investing these roots absorb water and minerals dissolved in it and pass it on to the coralloid roots and in turn receive food and growth substances from the root. Some of the hyphae enter inside the roots and remain in the intercellular spaces between the cells of the cortex.

In *Monotrapa*, a saprophytic seed plant, the mycorrhiza is ectotrophic as well as **endotrophic.** The hyphae form a compact pseudoparenchymatous investment around the root ; some of them enter the epidermal cells and crowd aside cytoplasm. The fungal attack modifies the epidermal layer.

This relationship appears to be obligate and attemps to grow pines in regions which lack these fungi have ended in a complete failure. The seeds of *Pinus* can, however, germinate in the absence of mycorrhizae.

In the orchids, the endophytic fungus is within cells. It occurs in the form of hyphal clusters in the cells. Some of the hyphae even enfold the nucleus. The seeds of orchids cannot germinate except in the presence of the mycelium, *Rhizoctonia.* It has no doubt been found that seeds can germinate non-symbiotically if sugar is supplied and pH regulated. It is believed that the fungus supplies vitamins to the orchids (Schofer, 1943).

In *Neottia*, the plant is devoid of chlorophyll and the fungal hyphae present in the cells in inner layers of the cortex are digested. As a result starch grains are produced which are found in abundance in the endodermis. The fungal hyphae are present in abundance and remain undigested in the cells in the outer layers of the cortex. The fungus takes ready-made food from the plant.

HALOPHYTES

Halophytes are those plants that occur naturally only on soils or in water too salty for the average plant. They grow in the salt marshes or along the margins of salt lakes and sea-shores, where the soil is rich in salt. In such places the soil is said to be **physiologically dry** because the water present in the soil is not available to the plants. Warming (1909) recognised two types of halophytes. These are : (*i*) *littoral swamp forests* or [illegible] (*ii*) *Psammophilous halophytes.* [illegible] and the roots cannot get oxygen. In such cases [illegible] ge[illegible] pne[illegible] [illegible] terised by the presence of numerous **lenticels** which serve to absorb air that goes to the roots below, through the intercellular spaces in the cortex. **Pneumatophores** are also present in *Sonneratia, Heritiera* and in the buttress roots of *Rhizophora.* The physiologically dry soil is rather

physiologically wet for the halophytes. Daubenmire defines the halophytes, *'They are ecologic group of plants characterised by an ability not only to endure high concentrations of certain ions in their water supply, but also to absorb water with ease under these conditions.'* The osmotic pressure of the halophytes varies with the salinity of their water supply.

The halophytes show xerormorphic characters especially succulence. In *Avicennia*, the leaves possess a subepidermal water storage tissue. A number of peltate hair are also present on the lower epidermis. These hair function as salt glands and excrete excess of salt-present in the absorbed water to the exterior.

Vivipary is also an important characteristic of the halophytes. It is the germination of seeds before the fruits have abscised. The germinated seeds develop roots and then fall on to the substratum. This saves the harmful effect of salt on germination.

Emersed halophytes are strikingly xerophytic in their features, palisade tissue being prominently developed, and often the epidermis is highly cutinised.

In *Salicornia*, a succulent halophyte, the stem possesses **storage tracheids** scattered in the subepidermal palisade layer in the stem. These are storage cells with thickened walls.

A few examples of both the types of halophytes are selected to illustrate their anatomical features.

Rhizophora mucronata Lamk. is the "true mangrove". It is very common along the outward and seaward edges of the swamp, where water is salty and the action of the tide is significant. It is a mediumsized tree that grows commonly in swamps along the sea coast in Bombay. It shows the following characteristics :—

Stem. (1) The young stem has a very thick cuticle (Fig. 17.21).

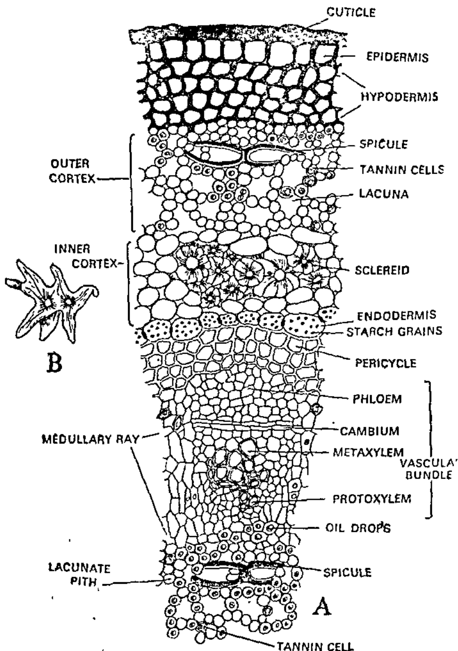
(2) The epidermal cells are almost squarish and are filled with tannin and oil.

(3) There is a well-developed hypodermis composed of 3—7 layers of thick-walled cells.

(4) The primary cortex is lacunar and acts as the chief aerating tissue (*Fig.* 17.21). The cells of the cortex have pitted walls and are full of tannin and oil. Crystals of calcium oxalate are also present in the cells. The lacunar (air spaces) cortex is strengthened by the presence of H-shaped spicules (*Fig.* 17.21) which occur singly in the outer layers of primary cortex. The arms of spicules project in the air-spaces or the lacunae. The walls of the spicules are lignified and act as mechanical supports for the soft cortex.

(5) The inner cortex possesses groups of branched sclereids (Fig. 17.21) that give an additional mechanical strength to the otherwise lacunate cortex. The arms of some of these sclereids hold tannin. The sclereids are highly lignified sclerenchymatous cells that are devoid

of cytoplasmic contents and have extremely narrow lumina (cell-cavities).



(Fig. 17.21. (A—B). A, *Halophytes*. T.S. young stem of *Rhizophora mucronata* Lamk., showing primary structure, It is a true mangrove plant. B, A branching sclereid from the cortex of A.

(6) Endodermis is clearly defined and its cells are packed with starch grains.

(7) The pericycle is sclerenchymatous and is made up of 3 or 4 layers of cells (Fig. 17.21).

(8) The pith is also lacunate (17.21) and its cells contain oil drops. A few tannin-filled cells are also present (Fig. 17.21).

(9) H-shaped spicules are present in the pith (Fig. 17.21).

(10) The cells in the medullary rays also store oil in the form of droplets. Tannin-filled cells are also present. The medullary rays are 2—3 seriate.

(11) The vascular bundles are conjoint, collateral, endarch and open.

(12) As a result of secondary growth, the stem develops sub-epidermal cork. Lenticels develop in older parts of the stem. The secondary cortex is also lacunate and contains both oil-filled and tannin-filled cells.

Petiole. The inner cortex of the petiole is lacunate and possesses H-shaped spicules. There is a ring of oval vascular bundles surrounding a medullary zone with intercellular spaces and H-shaped spicules. Scattered medullary bundles are also present in the medulla. A distinct endodermal layer is present as the last layer of the cortex. Tannin-filled and oil cells occur both in the cortex and the medulla or the pith.

Leaf. The leaf of *Rhizophora mucronata* shows the following anatomical features ;

(1) The cuticle is well-developed (Fig. 17.22) on both the leaf surfaces.

(2) The epidermal cells have thick and straight lateral walls.

(3) The cells in the upper epidermis are larger and hold some rod-shaped and cubical crystals of calcium oxalate.

(4) The stomata are confined to the lower epidermis. The stomata are considerably sunk below the outer leaf surface and have both outer and inner cuticular ridges (Fig. 17.22). The outer cuticular ridges are very prominent and are split so as to form a double chamber. The inner cuticular ridges are also prominent and are pressed against each other (Fig. 17 22). The guard cells are surrounded by subsidiary cells whose inner walls are thick (Fig. 17.22).

(5) Below the epidermis, there is a 3 to 4-layered tissue of large thin-walled cells that are filled with water. This is the subepidermal aqueous tissue (Fig. 17.22). The outer two layers of the aqueous tissue are, as a rule, full of tannin and oil. Large, elongated mucilage cells arise from inner face of aqueous tissue (Fig. 17.22) and are insinuated between the palisade cells.

(6) The palisade tissue is made up of three to four layers of elongated or columnar cells packed with chloroplasts (Fig. 17.22). Some columnar cells among the palisade cells are long and broad and contain tannin and oil. These are secretory cells.

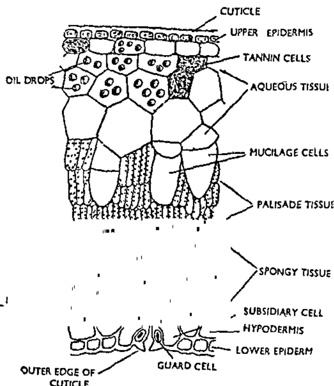


Fig. 17.22. V.S. Leaf of *Rhizophora mucronata* Note the aqueous tissue below the upper epidermis and calcium oxalate crystals in the cells of upper epidermis

(7) The spongy tissue is made up of 6—10 layers of thin-walled and loosely arranged chlorenchymatous cells.

(8) A single-layered hypodermal aqueous tissue also occurs on the under surface of the leaf (Fig. 17.22).

(9) On either side of the mid-rib the spongy parenchyma zone consists of star-shaped and small H-shaped thick-walled cells or sclereids.

(10) The leaves are dotted with black dots on both the surfaces. The dots are numerous on the ventral surface. These dots are cork warts or corky areas. These are made up of cork cells. The cork cells arise superficially at first but later on they penerate deep into the mesophyll tissue. The cork warts on the upper surface are larger in size and extend quite deep into the mesophyll, sometimes, reaching the spongy parenchyma.

Root. The plant bears stilt roots. The aerial or epigenous portions of roots and the subterranean portions of roots show many anatomical differences.

The subterranean roots have superficial cork layers that are made up of many layers of suberised cells. Here and there the compact corky stratum is interrupted by lenticels (Fig. 17.23). Next to the cork layer, there are one or few layers of secondary cortex. The primary cortex, which lies next to the secondary cortex, is very characteristic. The primary cortex is broad and lacunar (Fig. 17.23), being mainly modified as an aerating tissue. It is made up of two kinds of cells :—

(*i*) Stellate or star-shaped cells (Fig. 17.23), that are larger in number and are connected with each other by short, lateral arms. These cells are provided with peculiar thickening ridges (Fig. 17.23). These ridges are feebly lignified and give mechanical strength to the cells. Warming (1883) was of the opinion that these ridges are devices against side pressure.

(*ii*) The second type of cortical cells are narrow and tubular. They appear round or almost spherical in a cross-section. They occur at the junctions of stellate cells and are secretory in nature. They are full of tannin and oil. Multiradiate sclereids (Fig. 17.23) are also present in the primary cortex. They lend an additional support to the lacunate cortex.

The stele is contracted and there is a broad pith in the centre. The outer pith cells (perimedullary zone) are thick-walled and possess pitted thickenings. The thickening is lignin. These cells along with the thick-walled xylem elements form a strong central zone of mechanical tissue. Tannin cells and oil cells are present in the central part of the pith. Pericycle consists of secretory cells that occur in the form of arcs over the phloem groups.

In the aerial or the epigenous part of the stilt roots, the certex is lacunate and reduced. It is made up of one type of cells and is lacunate. There are no thickening ridges in the cortical cells. The cells are rounded. The cells contain oil drops and tannin. H-shaped spicules are also present in the cortex. Secretory cells are numerous in the pericycle. The stele is broad. The inner faces of xylem groups are strengthened by the presence of strongly lingnified sclerenchymatous cells. The pith is well-developed and possesses oil cells and tannin cells. H-shaped spicules are also present.

Sonneratia. It belongs to the family lythraceae. It is represented by two species in India. These are : *S. acida* and *S. apetala*. The former is very common in mangrove swamps, around Bombay. The latter rare, *S apetala* is a medium-sized tree with characteristic drooping branches and veinless leaves that look like phyllodes. It has also pneumatophores or breathing roots.

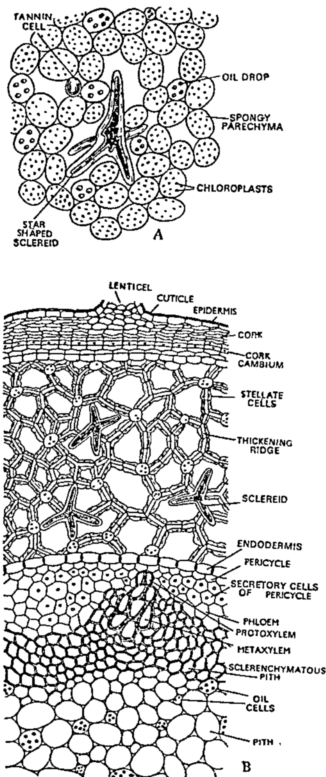


Fig. 17 23 *Rhizophora mucronata*. A, Spongy parenchyma cells around the mid-rib of leaf showing star-shaped sclereids, B, T.S. subterranean portion of the stilt root.

Root. The plant bears stilt roots. The aerial or epigenous portions of roots and the subterranean portions of roots show many anatomical differences.

The subterranean roots have superficial cork layers that are made up of many layers of suberised cells. Here and there the compact corky stratum is interrupted by lenticels (Fig. 17.23). Next to the cork layer, there are one or few layers of secondary cortex. The primary cortex, which lies next to the secondary cortex, is very characteristic. The primary cortex is broad and lacunar (Fig. 17.23), being mainly modified as an aerating tissue. It is made up of two kinds of cells :—

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(*ii*) The second type of cortical cells are narrow and tubular. They appear round or almost spherical in a cross-section. They occur at the junctions of stellate cells and are secretory in nature. They are full of tannin and oil. Multiradiate sclereids (Fig. 17.23) are also present in the primary cortex. They lend an additional support to the lacunate cortex.

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In the aerial or the epigenous part of the *stilt roots*, the certex is lacunate and reduced. It is made up of one type of cells and is lacunate. There are no thickening ridges in the cortical cells. The cells are rounded. The cells contain oil drops and *tannin*. H-shaped spicules are also present in the cortex. Secretory cells are numerous in the pericycle. The stele is- broad. The inner faces of xylem groups are strengthened by the presence of strongly lingnified sclerenchymatous cells. The pith is well-developed and possesses oil cells and tannin cells. H-shaped spicules are also present.

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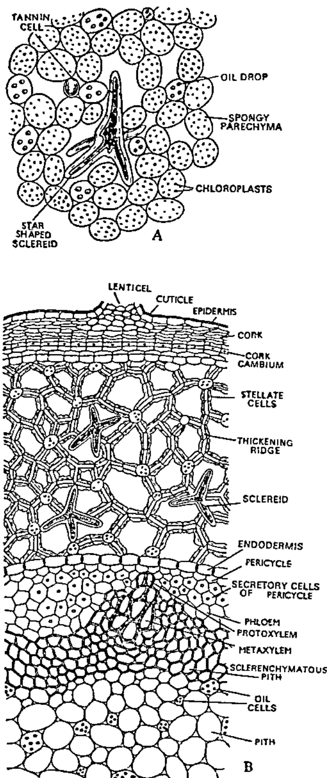


Fig. 17.23. *Rhizophora mucronata*. A, Spongy parenchyma cells around the mid-rib of leaf showing star-shaped sclereids B, T.S. subterranean portion of the stilt root.

In *S. apetala*, the stem is quadrangular in outline and has thick cuticle that is covered with grains of wax. The *epidermis is made* up of a single layer of cells that undergo secondary division i e, the mature epidermal cells sometimes divide *anticlinally* (Fig. 17.24). Below the epidermis is a hypodermis of collenchymatous cells. Collenchyma is well-developed below the *angles*. The rest of the cortex is made up of thin-walled cells that are loosely-arranged and enclose lots of *intercellular spaces* (Fig. 17.24). Elongated sclereids occur at the junction of the cortex and the hypodermis. These sclereids have thick and lignified walls and are branched at the ends (Fig. 17.24) Endodermis is not clearly distinguishable. The pericycle occurs in the form of patches over primary phloem. Intraxylary or internal phloem is also present next to xylem. The secondary phloem has vertical rows of crystal-containing cells. Next to the *internal* phloem is a row or two of secretory cells. The pith is lacunar and is supported by *multiradiate and* lignified sclereids. The cells of the pith and the cortex also contain *tannin* and oil drops. The cork arises subepidermally and is made up of lignified cells. The secondary cortex is composed of tangentially elongated cells. These cells also contain oil drops and tannin. Sclereids are also present in the secondary cortex.

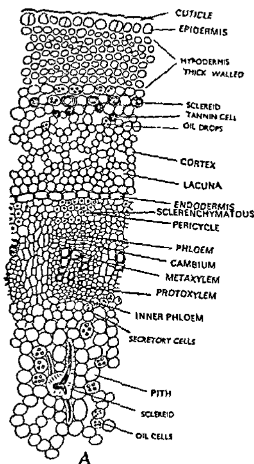


Fig 17.24. (A—B). A, T.S. young stem of Sonneratia apetala showing primary structure. Note the sclereids that appear rounded in a *transverse* section (cortex). The epidermal cells are undergoing secondary division.
B, L.S. portion of cortex showing the elongated sclereid with branched ends.

The leaf has stomata on both the surfaces (Fig. 17.5). The aqueous tissue *is central* (Fig. 17.25) in position. Large and circular mucilage cells are present below the upper epidermis (Fig. 17.23) and are *insinuated* into the palisade tissue. Branching tracheids and secretory cells are present in the aqueous tissue. Storage tracheids (Fig. 17.25) *also occur in the aqueous tissue.* Palisade tissue is also present on the lower

or ventral surface but its cells are less elongated. Tannin and oil cells also occur in the palisade cells. The stomata are deeply sunk and possess both outer and inner cuticular ridges. The upper epidermis is

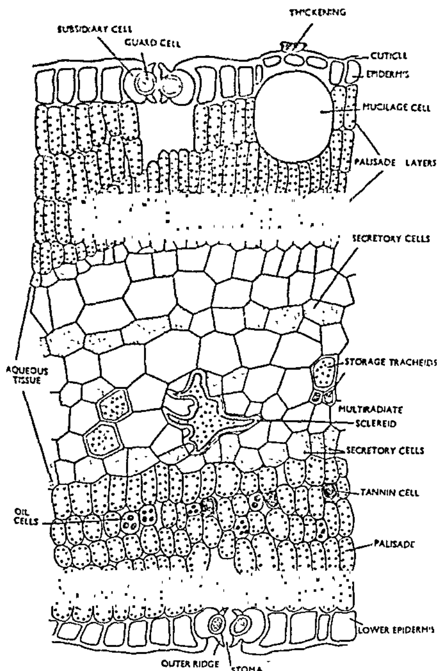


Fig. 17.25. T. S. Leaf of *Sonneratia apetala*. Note the centrally located aqueous tissue with sclereids and storage tracheids. A large mucilage cell has also been shown.

ribbed. The ribs are more prominent above the subepidermal mucilage cells and appear as rough wart-like structures in a cross-section. In

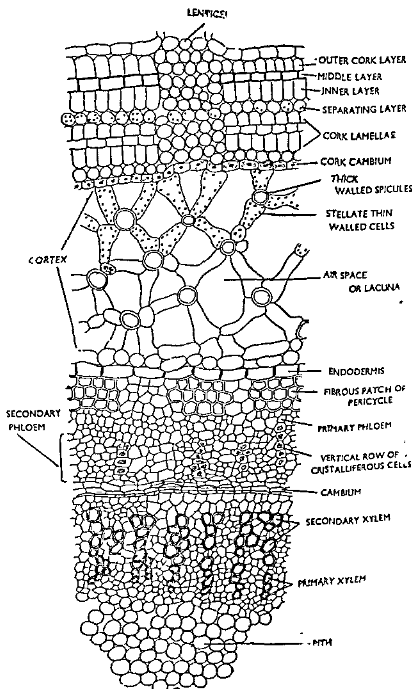


Fig. 17.26. *Sonneratia apetala.* T.S. portion of pneumatophore passing through proximal portion.

surface-view, the ribs appear as spine-like lumps. These ribs (Fig. 17.25) are made up of a fine meshed skeleton of a granular substance which dissolves slowly in KOH solution. Corky warts also occur on both the surfaces of the leaves of *S. apetala*. In *S. acida*, the epidermal cells also contain sphaeraphides (star-shaped crystals of calcium oxalate). These are absent in *S. apetala*. Blatter (1905) stated that the thickness of leaves in *S. acida* varies according to the habitat. Leaves are thicker in the plants growing in salt marshes.

The root system in *Sonneratia* consists of subterranean roots and aerial **pneumatophores** or breathing roots. The subterranean roots are soft and whitish in colour. Their anatomy resembles that of *Rhizophora* with slight differences. The cortex possesses characteristic vertically elongated thick-walled cells. The walls of these cells possess pitted thickenings. The thickening material is not lignin. The pith in older roots is lignified. In younger roots, only the perimedullary zone (outer pith) is lignified.

The pneumatophores possess a large number of lenticels. The cork layers are well-developed (Fig. 17.26). The cortex in the distal parts of the pneumatophore is made up of rounded cells that enclose large air-spaces (Fig. 17.27). The air spaces are schizogenous in origin in almost all mangrove plants. Chloroplasts may be present in the outer cells of the lacunate cortex. The cortex is strengthened by the presence of multiradiate sclereids that occur in abundance in the distal regions. Sometimes, the sclereids occur in groups. They give strength and support to the erect roots (Fig. 17.27). The sclereids are absent in the proximal portions of the root. The cortex in the proximal end of the root is lacunate (possesses air spaces) and is composed of triradiate or stellate cells and slightly curved and lignified spicules, that appear rounded in cross-section (Fig. 17.27). These spicules give strength to the cortex. Such spicules are absent in the distal ends of the root. The pericycle is made up of isolated patches of thick walled cells capping the phloem. Vertical rows of crystalliferous cells are present in the secondary phloem (Fig. 17.26). The pith in the distal region of the root possesses sclereids. In the proximal part sclereids are absent.

There are three layers of cork cells, the cells in the outer layer are rounded externally (Figs. 17.26, 17.27), those of middle layer are tubular or rectangular, whereas those of the innermost layer are radially elongated and have rounded inner edges.

In-between the cork layers there are one or two layers of separating cells that are almost round in *S. apetala* and *S. acida*. The cells of these layers are thin-walled. These cells have also been reported to contain chloroplasts and starch-grains.

Avecinnia. It is another mangrove plant of India belonging to the family verbenaceae. It is represented in Indian mangrove forests by two species (*A. officinalis* and *A. alba*). *Avecinnia officinalis* is also known as "white mangrove." The stem and the leaf show the same anatomical features as exhibited by *Rhizophora*. In *Avecinnia*, the stems and the leaves are covered with numerous trichomes (Fig. 17.28) and

glands (Fig. 17.28). The pneumatophores have also the same microstructure as found in *Sonneratia*. In *Avecinnia*, the pith of pneumatophores includes numerous large sclerenchyma cells.

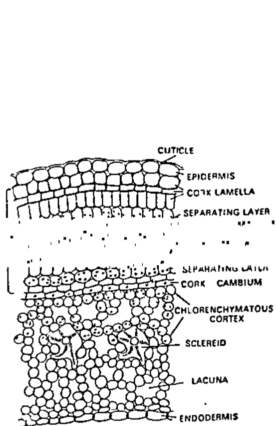


Fig. 17 27. *Sonneratia apetala*. T.S. through cortical region at the disdtal end of the pneumatophore showing cork layers and the cortex containing sclereids Lenticels and the central portion are not shown.

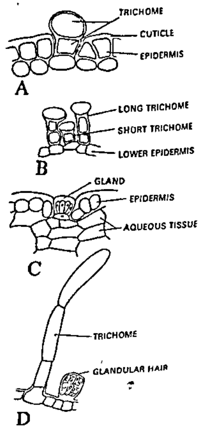


Fig. 17.28. (A—D) *Avecinnia*. Trichomes and glands, A, trichome from epidermis of stem. B, Short and long trichomes from the ventral surface of leaf C, A gland from upper surface of leaf. D, A trichome and gland from the petiolar groove.

The other common mangrove halophytes of India are : *Aegiceras majus*, *Acanthus illicifolius*, *Ceriops candolleana* and *Bruguiera caryophylloides*.

The second group of halophytes is called the *Psalmophytes*. They may be *annuals* or *perennials*. The annuals live and grow during the rainy season. They have not to face much difficulty as the perennials. They show less xerophytic characters. The perennials, on the other hand, show pronounced xerophytic features as they have to face the

intense insolation that prevails along the sea-shore during the drier periods of the year. They show the following chief characteristics :—

1. The leaves are generally reduced (*Suaeda fruticoa, Salsola foetida*) and their photosynthetic function is taken by the green stems.

2. The epidermis is covered by a thick cuticle and usually by a dense covering of hair or trichomes. Glandular hair are also present in abundance. Chalk glands and calcium secreting glands are also found in some. The stomata are usually sunken. The cuticle may also be covered with a coating of wax.

3. The stem is ridged and the chlorophyllose cells of the cortex are usually restricted below the grooves *e.g., Leucas aspera, Celosia argentea*. The cells are always placed at right angles to the exposed surface. They are elongated and palisade-like.

4. The pith in some cases gets lignified or sclerosed.

5. Epidermal cells in some cases get enlarged and store water *e.g. Suaeda nudiflora, Sesuvium portulacastrum*.

6. In *Suaeda nudiflora*; the older leaves have a well-developed aqueous tissue in the centre. The palisade tissue in these leaves is less developed. These older leaves serve as water-storage organs for the younger leaves.

7. *Suaeda nudiflora* is also characteristic in having deep-seated chlorenchyma. The cells of the inner cortex, endodermis, some cells in the vascular bundles and even the pith cells possess chloroplasts.

8. The epidermal cells and sometimes the cells in the hypodermis and cortex are filled with anthocyanin pigments. Oil storing and tannin-filled cells are also very common in the perennial Psalmophyllous halophytes. Presence of tannin is regarded by Warming (1883) to save the tissues [illegible] hygroscopic. [illegible] gor pressure [illegible] ells has been [illegible] to desiccation.

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